Dynamics of a Socially and Spatially Structured Giraffe Population in a Human-Natural Landscape

Dissertation

zur

Erlangung der naturwissenschaftlichen Doktorwürde

(Dr. sc. nat.)

vorgelegt der

Mathematisch-naturwissenschaftlichen Fakultat

der

Universität Zürich

von

Monica Louise Bond

von

Luzern LU

Promotionskommission
Prof. Dr. Barbara König (Vorsitz und Leitung)
Prof. Dr. Arpat Ozgul
Dr. Damien Farine

Zürich 2020

Acknowledgements

The field research for this PhD was conducted with permission from the Tanzania Commission for Science and Technology, Tanzania National Parks, the Tanzania Wildlife Research Institute, Tanzania Wildlife Authority, and Manyara Ranch Conservancy.

I am thankful for financial support for the PhD provided by the University of Zürich's University Research Fund (Forschungskredit), Parrotia-Stiftung, Temperatio-Stiftung, and the Wild Nature Institute. Field work in Tanzania was funded by Sacramento Zoo, Columbus Zoo and Aquarium, Tulsa Zoo, Tierpark Berlin and Zoo Berlin, Cincinnati Zoo and Botanical Garden, Como Friends, Zoo Miami, African Wildlife Foundation, Save the Giraffes, Promotor Foundation, Claraz Foundation, and the University of Zürich Graduate Research Campus.

I am deeply grateful for the invaluable mentorship of my PhD committee members Barbara König, Arpat Ozgul, and Damien Farine. Claudia Huonder Döring provided essential administrative support. Mara Knüsel did an excellent job helping with chapter 6. I would also like to thank my family, particularly Bob and Irma Bond and Max and Joan Lee, for their loving encouragement and assistance while I lived abroad. I gratefully acknowledge the pioneer in the field of giraffe research, Anne Innis Dagg. Finally, this PhD would not have been possible without Derek Lee, my colleague and life partner, who worked together with me to set up the long-term giraffe demography project in Tanzania, obtain all research permissions, and collect field data, and who provided constructive statistical advice and moral support throughout this process.

This PhD is dedicated to the memory of Wayne Lotter, a true wildlife hero and forever my inspiration.

Summary

Sociality involves a constant trade-off between fitness benefits and costs of living in groups, and this trade-off can be influenced by the social and ecological environment in which individuals live. In this PhD I explored socioecological factors underlying the social and spatial population structure and dynamics of a large tropical herbivore with a highly fission-fusion social system, the giraffe (*Giraffa camelopardalis*). Using a dataset of more than 3,000 uniquely identified individuals collected over a period of 8 years in the coupled human-natural Tarangire Ecosystem of northern Tanzania, I (1) investigated natural and anthropogenic factors as mechanisms of giraffe grouping dynamics, social structure, space use, and vital rates; (2) quantified fitness consequences of social behaviours of adult female giraffes in relation to the influence of their physical environment; and (3) compared social versus spatial dispersal of subadult female and male giraffes. I used capture-mark-recapture techniques to estimate survival rates while accounting for imperfect detection, and social network analysis to derive network- and individual-level social metrics and to delineate discrete communities of socially associated adult female giraffes within a larger contiguous metapopulation. Natural and anthropogenic factors included vegetation types and preferred plant forage species, natural predation, and distance to traditional (bomas) and modern human settlements (towns). I found that grouping patterns of giraffes were influenced by food availability, predation risk, and presence of humans, with particular requirements for mothers with calves (chapter 1). I parsed the metapopulation into 14 distinct, modular yet overlapping communities of socially associated adult female giraffes, with 11 communities large enough to test hypotheses explaining variation in social structure (chapter 2). Adult females in communities closer to bomas had weaker relationship strengths among all members of the community and more exclusive relationships with fewer other females,

suggesting that the presence of humans disrupted their social structure. In an examination of social versus ecological drivers of variation in reproduction and survival among 10 of the communities, I showed demographic rates were correlated with vegetation and proximity to humans, as communities with more dense bushlands had lower calf survival while those closer to human settlements had higher reproductive rates (chapter 3). Adult female survival did not differ among communities (chapter 3), but more gregarious females (being in larger groups) and females with higher betweenness (associated with more groups) had higher survival (chapter 4). Survival of adult females is improved by being well-integrated into their larger social community through having weaker bonds with many others rather than by forming stronger and highly stable bonds with just a few individuals. This suggests that the disruption of social structure close to bomas as evidenced in chapter 2 could have demographic consequences, although proximity to bomas did not influence adult female survival as much as their level of sociability (chapter 4). In chapter 5, I investigated patterns of natal dispersal, and found that while most young males dispersed into new social communities far from where they were first detected as calves, many shifted into new communities that were close to their natal areas. In contrast, few young females dispersed, but those that did disperse rarely shifted into a new social community. Instead females moved spatially while remaining within their natal community, further demonstrating the importance of maintaining social ties, from calf to adulthood, across their community of associates. Human presence influenced space use of adults, as adult females living closer to densely populated towns had significantly larger home ranges, but no such relationship was evident with bomas, indicating a difference in anthropogenic impact on movements of giraffes between traditional versus modern human lifestyles (chapter 6). My research indicates that social associations among individuals in addition to ecological conditions are likely to be important for

population persistence, and should be considered when developing and implementing conservation measures for giraffes such as land-use plans and translocations.

Zusammenfassung

Soziale Tiere befinden sich in einem ständigen Zielkonflikt zwischen den evolutionären Nutzen und Kosten des Gruppenlebens. Dieser Zielkonflikt kann entscheidend durch das soziale und ökologische Umfeld der Individuen beeinflusst werden. In dieser Doktorarbeit untersuchte ich sozial-ökologische Variablen, die der sozialen und räumlichen Populationsstruktur und Populationsdynamik von Giraffen (*Giraffa camelopardalis*) zu Grunde liegen. Giraffen sind große, tropische Pflanzenfresser, und mit ihrem „fission-fusion" Sozialsystem sind sie für eine derartige Studie ideal geeignet. Basierend auf Daten von über 3000 identifizierten Individuen, die über 8 Jahre im Tarangire-Ökosystem im Norden Tansanias gesammelt wurden, (1) untersuchte ich natürliche und anthropogene Faktoren als Mechanismen für Gruppendynamik, Sozialstruktur, Raumnutzung, und Überlebensraten von Giraffen; (2) quantifizierte ich Fitnesskonsequenzen des Sozialverhaltens adulter, weiblicher Giraffen in Bezug auf ihre physische Umwelt; und (3) verglich ich das soziale und räumliche Abwanderungsverhalten subadulter, weiblicher und männlicher Giraffen. Um Überlebenswahrscheinlichkeiten abzuschätzen, wandte ich Fang-Wiederfang Methoden unter Berücksichtigung imperfekter Entdeckungswahrscheinlichkeiten an. Zur Abschätzung von Netzwerk-Parametern und individueller sozialer Kennzahlen sowie zur Abgrenzung diskreter Sozialverbände weiblicher Giraffen innerhalb der weiteren Metapopulation, verwendete ich soziale Netzwerkanalysetechniken. Natürliche und anthropogene Faktoren beinhalteten den Vegetationstypus, bevorzugte Futterpflanzen, natürliche Prädation, sowie Entfernung zu traditionellen („Bomas") und modernen (Städte) menschlichen Siedlungen. Die Gruppenstruktur der Giraffen wurde durch Futterangebot, Prädationsrisiko und Anwesenheit von Menschen

beeinflusst; diese Einflussgrößen spielten vor allem für Giraffenmütter und ihre Kälber eine große Rolle (Kapitel 1).

Ich teilte die Metapopulation in 14 verschiedene, modulare, aber überlappende Gemeinschaften assozierter adulter, weiblicher Giraffen, und ich testete anhand von 11 ausreichend großer Gemeinschaften Hypothesen zur Erklärung der variierenden Sozialstruktur (Kapitel 2). Adulte Weibchen in geringer Entfernung zu Bomas hatten schwächere Sozialbindungen mit allen Giraffen in ihrer Gemeinschaft und eher exklusivere Assoziationen mit wenigen Weibchen der Gruppe. Dies deutet darauf hin, dass die Sozialstruktur von Giraffen möglicherweise durch Menschen gestört wird. In einer weiteren Studie untersuchte ich, ob soziale oder ökologische Faktoren die beobachtete Variation der Reproduktions- und Überlebensraten innerhalb der 10 Giraffengemeinschaften erklären können. In dieser Studie zeigte ich, dass Überlebens- und Fortpflanzungsraten mit der Vegetationstruktur sowie mit der Entfernung zu menschlichen Siedlungen korreliert waren: Giraffengemeinschaften in Gebieten mit einem hohen Anteil dichter Buschvegetation waren durch niedrige Überlebenswahrscheinlichkeiten der Kälber gekennzeichnet, während Giraffengemeinschaften in der Nähe menschlicher Siedlungen hohe Reproduktionsraten aufwiesen (Kapitel 3). Obwohl die Überlebenswahrscheinlichkeiten adulter, weiblicher Giraffen nicht zwischen den Gemeinschaften variierte (Kapitel 3), hatten sozialere Weibchen (Weibchen in größeren Gruppen) und Weibchen mit einer größeren Zwischen-Kennzahl („betweenness“, das heisst, mit mehreren Gruppen assoziiert) größere Überlebenswahrscheinlichkeiten (Kapitel 4). Die Überlebenswahrscheinlichkeit weiblicher, adulter Giraffen steigt folglich, wenn sie innerhalb der Gemeinschaft gut integriert sind und viele, eher schwächere Bindungen mit vielen Individuen haben, aber nicht unbedingt, wenn sie wenige, stabile Bindungen mit einzelnen Individuen eingehen. Dies deutet darauf hin, dass gestörte Sozialstrukturen in der Nähe menschlicher Siedlungen (wie in Kapitel 2 beschrieben)

demographische Konsequenzen nach sich ziehen könnten, obwohl die Entfernung zu Bomas die Überlebenswahrscheinlichkeit nicht in demselben Maße beeinflusst, wie sie die Sozialität beeinträchtigt (Kapitel 4).

In Kapitel 5 untersuchte ich Muster des Abwanderungsverhaltens junger Giraffen. Die meisten jungen Männchen wanderten zuerst in eine andere Sozialstruktur ab, die weit entfernt von den Gebieten lagen, in denen sie erstmalig als Kälber erfasst wurden. Interessanterweise kehrten jedoch viele der jungen Männchen in die Nähe ihrer Geburtsgebiete zurück. Demgegenüber wanderten nur wenige der jungen Weibchen ab. Die wenigen dispergierenden Weibchen wechselten auch nur selten in neue Gemeinschaften. Weibliche Giraffen bewegten sich stattdessen primär räumlich, aber innerhalb ihrer Geburts-Gemeinschafen. Dieses Verhalten zeigt wiederum die große Bedeutung der Sozialstrukturen – von der Geburt bis zum Erwachsenwerden – innerhalb der Giraffengemeinschaften. Die Nähe zu menschlichen Siedlungen beeinflusste die Raummnutzung adulter Giraffen: Streifgebiete weiblicher, adulter Giraffen waren signifikant größer in der Nähe dichtbesiedelter Städte. Da die Entfernung zu traditionellen Siedlungen (Bomas) jedoch keinen Einfluss auf die Streifgebietsgröße hatte, scheinen moderne und traditionelle menschliche Lebensstile unterschiedliche Auswirkungen auf das Raumverhalten der Giraffen zu haben (Kapitel 6). Meine Forschungsergebnisse deuten darauf hin, dass soziale Assoziationen zwischen Individuen und ökologische Bedingungen gleichermaßen wichtig für die Langlebigkeit von Giraffenpopulationen sind. Bei der Entwicklung und Umsetzung von Strategien zum Schutz von Giraffen, wie z.B. Landnutzungspläne und Translokationen, sollten diese Erkenntnisse möglichst beachtet werden.

Table of Contents

Introduction

Sociality involves individuals living and interacting together, which leads to complex relationships and multi-level structure of populations (Alexander 1974, Krause and Ruxton 2002, Whitehead 2008b, Clutton-Brock 2016). Social structure arises in a population when individuals form preferred and avoided relationships (Whitehead 2008b). Social relationships involve a constant trade-off between fitness benefits of living in close proximity to conspecifics, such as reduced predation risk, cooperative care of offspring, increased probability of winning inter-group competition, and information sharing, and the costs, including disease and parasite transmission or local resource competition for food and mates (Alexander 1974, Majolo et al. 2008, Markham et al. 2015). This trade-off can be influenced by the ecological environment in which individuals live.

Social ecology is a framework for understanding relationships among social and ecological factors. The primary goal of socioecological theory from a wildlife perspective is to explain social relationships, grouping patterns, mating behaviour, habitat use, and dispersal tendencies, as adaptive responses to features of the social and ecological environment (Aureli et al. 2008). Central questions for advancing socioecological theory include: how do social and environmental variables influence social behaviours and subsequent fitness? How do social behaviours mediate population dynamics? How can this information be used to effectively conserve species in the face of threats such as human disturbances?

The study of demography—births, deaths, and movements—can elucidate how socioecological factors drive population dynamics, which in turn is critical for successful management and conservation of wildlife. Variation in demographic vital rates plays a major role in determining population viability (Pulliam 1988, Rodenhouse et al. 1997, Hanski 1999). Management and conservation of species, subspecies, or populations can be facilitated by

understanding how and why populations are structured, and how and why demographic vital rates vary among populations. This is especially important for declining populations that are hunted or that inhabit fragmented landscapes subject to human activities, because specific anthropogenic factors implicated in population declines can be identified and potentially ameliorated as human influences intensify (Ceballos et al. 2017).

Behaviours such as foraging, mating, cooperation and grouping, and predator avoidance can influence demographic vital rates of movements, survival, and reproduction, which in turn underlie population dynamics and fitness (Fig. 1). Recognizing and monitoring individual animals allows researchers to describe social behaviour, estimate vital rates, and quantify fitness (Clutton-Brock and Sheldon 2010). Because social behaviour can have fitness consequences, integrating the study of behaviour with demography leads to a deeper understanding of mechanisms driving social and spatial population structure, and informs conservation and management decisions (see e.g. Bremner-Harrison et al. 2004, Shier 2006).

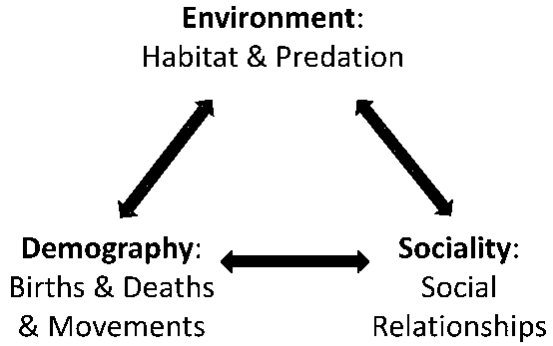

Figure 1. Interconnections among the environment, sociality, and demography

The goals of this dissertation are to better understand the evolution of social systems by integrating the study of social behaviour and demography, and to investigate environmental factors underlying the social and spatial population structure and dynamics of a large tropical herbivore with a fission-fusion social system, the giraffe. I do so by analysing eight years of

continuous, systematically collected photographic capture-recapture data from thousands of individually identified giraffes in the coupled human-natural Tarangire Ecosystem of Tanzania, East Africa. Results from this research will have important implications for understanding the social system and population dynamics of this African icon as well as other tropical ungulates and potentially other taxa that exhibit fission–fusion social dynamics. Novel aspects of this research include investigating environmental factors as mechanisms of giraffe social structure, grouping dynamics, and space use; quantifying fitness consequences of social behaviours of adult female giraffes in relation to the influence of the physical environment; and comparing social versus spatial dispersal of subadult female and male giraffes.

RESEARCH QUESTIONS

(1) ***How do environmental and social variables influence size and composition of giraffe groups?*** Spatial and temporal heterogeneity in food resources and predation risk can bring about group fission–fusion dynamics across space and time. In chapter 1, I examine the effects of natural (lion density, vegetation structure, and prevalence of primary forage plants), anthropogenic (proximity to human settlements), temporal (rainy or dry season and time of day), and social factors (local giraffe density, adult sex ratio, and proportion of calves) on giraffe group size and composition, to test predictions derived from previous studies about the relative influence of food availability versus predation risk on fission-fusion dynamics in a wild herbivore.

(2) ***How do natural and anthropogenic variables influence social structure in giraffe populations?*** Humans might indirectly influence dynamics of wild populations through repeated disturbances that affect social interactions. In chapter 2, I examine whether social communities of giraffes living closer to human settlements exhibit weaker association strengths and more exclusive social associations—a signature of a disturbed social environment.

(3) ***Do demographic parameters vary among communities of giraffes, and do environmental and social variables explain any observed variation?*** A critical question in wildlife management and population biology is how populations should be defined,

and what are the relative demographic influences of the social versus physical environment. In chapter 3, I compare demography among spatially overlapping yet distinct social communities of female giraffes to explore social and environmental drivers of life-history variation. This is the first study to examine demographic variation among social communities as defined by social network analyses, for any ungulate species.

(4) ***How do social tendencies of individual giraffes influence their survival?*** The extent to which social interactions between individuals drives variation in their survival, in conjunction with their physical environment, remains largely unexplored in wild mammalian societies. In chapter 4, I quantify the relative contributions of sociability (gregariousness, relationship strength, and betweenness), the natural environment (vegetation types), and anthropogenic pressures (distance to human settlements) on adult female giraffe survival rates to gain a deeper understanding of the evolution of the giraffe's social system.

(5) ***How do environmental and social variables affect natal dispersal of giraffes?*** Dispersal is a critical parameter that influences individual fitness, gene flow, adaptation to local conditions, inbreeding, population size, colonization, and persistence of populations and species. In chapter 5, I describe and estimate natal dispersal in giraffes, and test hypotheses related to dispersal propensity, dispersal age, and distance moved for both male and female subadults. I also compare social versus spatial dispersal patterns to examine whether individuals can disperse to new communities while remaining in their natal range.

(6) ***How do natural and anthropogenic factors influence space use of giraffes?*** Abiotic, biotic and human influences are factors that can affect animal home ranges. In chapter 6, I quantify home ranges and model home range size as a function of natural and anthropogenic predictors, to better understand mechanisms driving space use by giraffes in our study ecosystem and across Africa.

STUDY SPECIES

Giraffes (*Giraffa camelopardalis*: Fig. 2) are endemic African ruminants, and one of only a handful of extant terrestrial megaherbivore species, defined as animals reaching up to 1,000 kg in mass (Owen-Smith 1988). They are sexually dimorphic, iteroparous, non-territorial, browsers

that feed mostly on leaves, twigs, flowers, and fruits of *Acacia*, *Balanites*, *Dichrostachys*, and many other species of woody vegetation (see references in Dagg 2014).

Giraffes are long-lived (approximately 25–28 yr; Dagg and Foster 1976) and slow breeding; females in the wild become sexually mature at a mean of 4.8 years of age (Bercovitch and Berry 2009) and mean gestation period is 14.7 months (del Castillo et al. 2005), thus they bear their first offspring at ~6 years of age, with a mean subsequent interbirth interval of 20 months (Strauss et al. 2016).

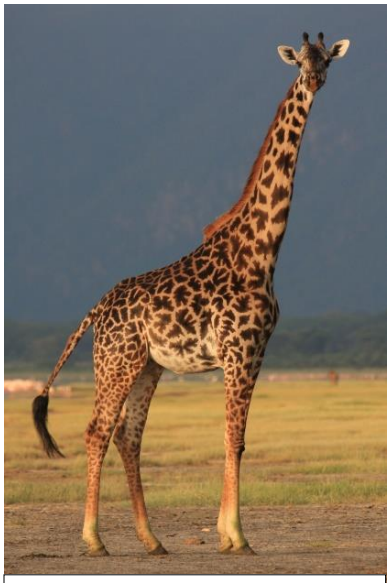

Figure 2. Adult female Masai giraffe, Lake Manyara National Park, Tanzania

Females reproduce throughout the year, and can become pregnant while still nursing their previous offspring (Dagg and Foster 1976, del Castillo et al. 2005, Lee et al. 2017). The energetic costs of motherhood are adjusted during pregnancy so that during the first trimester of pregnancy fetal growth is slow and maximum effort is spent on nursing the previous calf; energetic effort is then shifted in the last trimester toward fetal growth as the previous nursing calf is weaned (del Castillo et al. 2005). The age at weaning is 15–18 months (Leuthold 1979) but calves spend more time browsing than suckling after four months of age (Pratt and Anderson 1979). Previous studies indicated mothers with calves tend to feed more in open areas, while pregnant females are found in more densely vegetated habitats which might be either an anti-predator strategy involving hiding very young calves, or a strategy for decreasing tannin intake (Young and Isbell 1991, Fursternburg and van Hoven 1994, Caister et al. 2003).

The giraffe's life history of delayed maturity and longevity means that survival of breeding adult females is the highest elasticity parameter in population growth rate models (Lee et al. 2016a, Strauss et al. 2016). The giraffe's primary natural predators are African lions

(*Panthera leo*), leopards (*Panthera pardus*), and spotted hyenas (*Crocuta crocuta*) (Dagg and Foster 1976). Predation by lions is an important limiting factor for juvenile survival (Strauss et al. 2015, Lee et al. 2016a) but only a minor source of adult giraffe mortality (Schaller 1972, Strauss and Packer 2013). However, adult giraffes are killed by bushmeat poachers (Ndibalema and Songorwa 2007, Kiffner et al. 2015) which was implicated in local population declines (Strauss et al. 2015, Lee et al. 2016a).

Giraffe social structure is described as a fission–fusion process whereby herd composition varies but is structured based on non-random social associations between adult females that reflect kinship (Berkovich and Berry 2012, Carter et al. 2013a). The social system of giraffes is similar to other fission–fusion animal societies including some primates, bats, dolphins, elephants, ungulates, and spotted hyenas (see references in Aureli et al. 2008). Studies of this megaherbivore can elucidate general applicability of patterns observed in studies of smaller-bodied species by providing an allometric endpoint for comparison and contrast.

Giraffe populations in central and East Africa have declined precipitously (Muller et al. 2016; see Fig. 3 for distribution). A deeper understanding of how social and environmental variables influence behaviours and population dynamics will aid in developing effective conservation measures for this African icon. Further, the vast majority of the world's hoofed mammals live in tropical regions (Owen-Smith and Marshall 2010), yet most studies of ungulate demography have been conducted in temperate regions (Gaillard et al. 2000). Research in the tropics is urgently needed as human populations there continue to expand at a higher rate than anywhere else in the world (United Nations 2015).

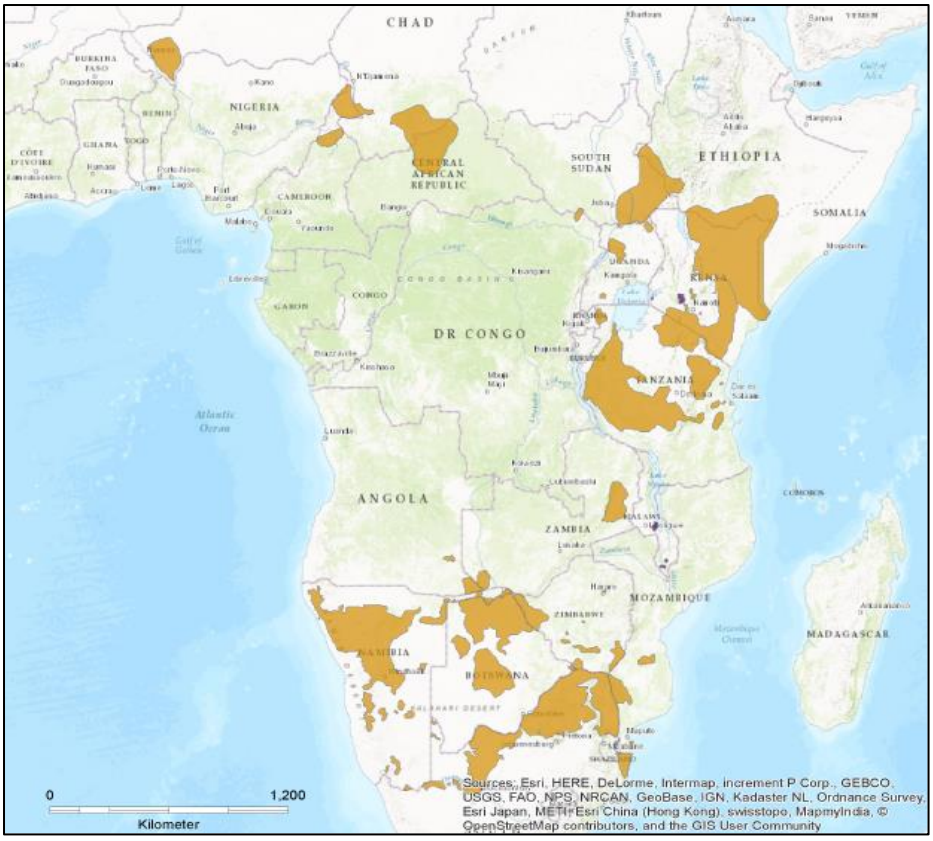

Figure 3. Distribution of giraffes (*Giraffa camelopardalis*). From Muller et al. (2016)

HISTORY OF DEMOGRAPHIC AND SOCIAL RESEARCH ON GIRAFFES

Giraffes are an excellent study species for socioecological demographic research because they are easily detected and photographed for identification. Indeed, Pratt and Anderson (1985; p. 771) noted:

> "Many features recommend the giraffe for behavioural study: it is big, abundant, conspicuous, active by day, reasonably trusting of people, deliberate, and the best self-marked animal in existence."

The technique of using photographs to recognize individual giraffes from their unique and unchanging spot patterns was pioneered by Bristol Foster in the 1960s (Dagg 2014). Based upon this technique, in the 1970s and early 1980s demographic rates were estimated from simple return rates of relatively small numbers of known animals (Foster and Dagg 1972, Leuthold and Leuthold 1978, Pellew 1983). Since that time, ever more sophisticated statistical methodologies

(e.g. Lebreton et al 1992, Nichols 1992, Pradel 1996) and computer programs (e.g., MARK; White and Burnham 1999) have become available to robustly estimate demographic parameters from capture-recapture data while accounting for imperfect detectability. However, demographic research on giraffe populations using these statistical methodologies has only recently been conducted (Lee and Strauss 2016). The advancement of two technologies, digital photography and pattern-recognition software, has facilitated analyses of unprecedented large sample sizes of giraffes and greatly advanced scientific knowledge of the species' demography and social behaviour (Bolger et al. 2012).

Researchers in Tanzania in East Africa have led the world in publishing demographic studies on giraffes using these new technologies and statistical methodologies. The Masai giraffe (*G. c. tippelskirchi*) is the most numerous of nine subspecies (Muller et al. 2016), with the majority residing in Tanzania. Two projects, both conducted over the course of three years, estimated demographic rates of Masai giraffe using the computer pattern-matching program Wild-ID (http://software.dartmouth.edu/Macintosh/Academic/Wild-ID_1.0.0.zip). Wild-ID matched a large test dataset of giraffe images with a low false rejection rate (0.0007) and 0.0 false acceptance rate (Bolger et al. 2012) and thus works extremely well for this species. Strauss et al. (2016) estimated reproduction and age-specific survival in three giraffe sub-populations (n = 771 adults/subadults and 146 calves) in the Serengeti Ecosystem, and documented declining population growth rates which might be attributed to poaching and limited food resources. Lee et al. (2016a) estimated reproduction, age-specific survival, and movement rates of 860 adult female giraffes in five giraffe subpopulations defined by management authority in the Tarangire Ecosystem, and reported lower adult female survival in subpopulations with high densities of people. Lee et al. (2017) also found that survival of giraffe calves (n = 449) born in the dry season experienced the highest survival, and Lee et al. (2016b) quantified that giraffe neonatal

and calf survival probabilities were higher when the migratory herds of eastern white-bearded wildebeests (*Connochaetes taurinus albojubatus*) and plains zebras (*Eqqus quagga*) were present, suggesting the presence of alternative prey deflected predation on giraffes. These studies provided robust estimates of the various components of the demographic processes, some possible ecological and anthropogenic factors driving those processes, and potential selective forces.

In addition to the study of demography, researchers have used the unique markings of giraffes to identify individuals and describe their social relationships. Early studies reported continual turnover in group composition and lack of close ties between individuals (Foster and Dagg 1972, Leuthold 1979, van der Jeugd and Prins 2000, Le Pendu et al. 2000). In contrast, Pratt and Anderson (1985) were the first researchers to suggest a relatively stable structure of female Masai giraffe herds composed of a few mothers with calves, usually of a similar age, that 'chose' to remain together. The same relatively recent technologies of digital photography and pattern-recognition software that aided demographic research have also improved the study of social dynamics of giraffe populations. Shorrocks and Croft (2009) conducted a study of 133 individually recognized reticulated giraffes (G. *c. reticulata*) in Kenya to demonstrate the utility of using computer programs to describe social networks of giraffes. Two subsequent projects calculated network matrices of several hundred individually recognized giraffes using different computer programs to describe social networks. Carter et al. (2013a) found Angolan giraffes (*G. c. angolensis*) in Namibia's Etosha National Park showed definite preferred and avoided relationships among 266 females, but not among 269 males. In a subsample of 47 females (varying ages from juvenile to adult) the authors used genetic data to document that giraffes in 'preferred' relationships were more related to each other than expected from random associations, and avoided unrelated females. A second study comparing social networks of this

Namibian population over two time periods demonstrated stability of relationships of 243 female pairs over three years, but no long-term associations among males, and young females increased their number of associations as they aged and then stabilized their social connectivity (Carter et al. 2013b). VanderWaal et al. (2014) identified community structure at multiple scales for 170 individually recognized reticulated giraffes (86 females and 84 males) at Ol Pejeta Conservancy in Kenya over a 6-month period. Community structure algorithms identified three hierarchical levels of clusters whereby social 'cliques' were embedded in 'sub-communities' which in turn were embedded in 2 larger 'communities.' Younger males had stronger associations with males of the same age group than with older males, and older males had lower associations with older males than with younger males. Female social organization was closely tied to shared space use, but this was not the case for male communities (VanderWaal et al. 2014). Muller et al. (2018) studied two populations of 77 and 89 individually recognized Rothschild's giraffe (*G. c. rothschildi*) in adjacent protected areas and documented that the strength of social affiliations was influenced by whether the animals were traveling, foraging, or resting, and differed by habitat density and disturbance levels. Further, the social network structure of these two populations appeared to differ, although differences between the networks were not compared statistically (Muller et al. 2019). A social network of 167 giraffes in South Africa's Pilanesberg National Park constructed separately in three wet and two dry seasons showed giraffes had stronger social connectedness and more social ties (i.e. larger group sizes) during the wet season (Prehn et al. 2019). These studies provided the most robust analyses ever conducted on the social networks of giraffes, and offer an excellent foundation for new socioecological research. The next step is to test hypotheses to explain how and why social structure and demography vary among giraffe social communities, and how social and ecological variables synergistically influence fitness and movements.

STUDY DESIGN

Each giraffe has a coat pattern that is unique and unchanging from birth to death. Together with my research team, we photographed, and later identified individual giraffes from their unique coat markings. From June 2011 until October 2018, we conducted 42 daytime, fixed-route road transect surveys to collect photographic capture-recapture data on three primary sampling periods per year near the end of each precipitation season (Jan–Feb, May–June, and Sep–Oct). We sampled according to a robust design with each primary sampling period composed of two independent, back-to-back secondary sampling periods during which all road transects in the study area were driven once (Pollack 1982; Fig. 4), for a total of 6 independent surveys per year. Road density throughout the study area was high (0.42 km/km^2) relative to average adult female giraffe home range (115 km^2; Knüsel et al. 2019). We maintained driving speed between 15 and 20 km on all transects, and all surveys included the same two observers. Each primary sampling period took approximately 21 days.

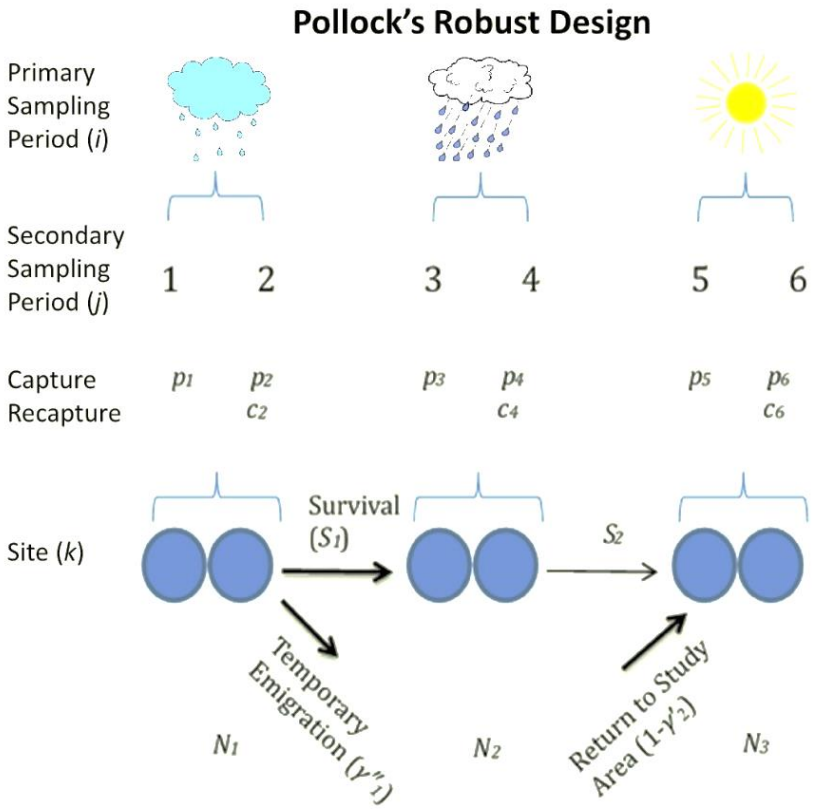

Figure 4. Diagram of Pollock's Robust Design statistical capture-mark-recapture model and parameters during one calendar year (three primary sampling periods = short rains, long rains, dry). Each blue circle represents a secondary sampling period during which all road transects are driven.

When giraffes were encountered, we 'marked' (or resighted) each animal by photographing them on the right side for individual identification. For each photograph, we recorded the animal's age class (calf, subadult, adult), sex (male, female), and GPS location. We used physical characteristics, including body shape, relative length of the neck and legs, ossicone characteristics [the ends are knobbed and hairless in adult males, while ends are thin and tufted in females and young], and height to categorize giraffe into three age classes: calf (<1 year), subadult (1–3 years), or adult (>3 years). We measured the distance from the camera to each animal using a laser range finder, and I later estimated height from the camera focal length and

photogrammetric measurements to objectively age each animal based on height. Lastly, we noted the size of the herd, defined as all animals within 500 m of each other.

To identify individuals, I utilized Wild-ID (Fig. 5), a computer program that matches unique patterns from photographs. The program uses the Scale Invariant Feature Transform (SIFT) algorithm implemented in a Java platform to find and extract image features invariant to image scale, rotation, viewpoint, local distortion, and illumination (Bolger et al. 2012). This system is known to perform with little misidentification error in large giraffe datasets (Bolger et al. 2012). I created individual encounter histories for three life history stages: adults, subadults, and calves. I used social network analysis to partition the adult female giraffe metapopulation in the Tarangire Ecosystem into social communities and to generate individual and network-level measures of sociality among communities and individuals.

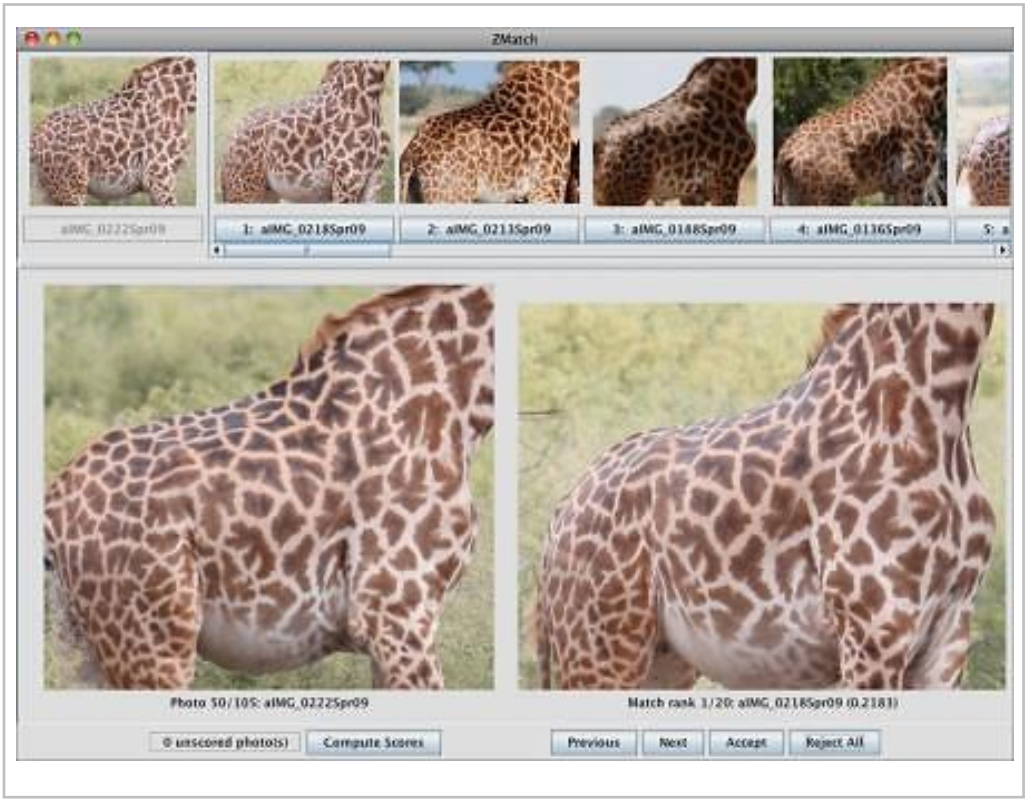

Figure 5. Screen shot from the Wild-ID program demonstrating a matched giraffe coat pattern.

I then developed and tested the influence of a suite of spatial environmental and social covariates on grouping dynamics, social structure, space use, and vital rates.

Environmental covariates included:

1. Vegetation structure (open to dense) and preferred giraffe forage plants (*Acacia tortilis*, *A. drepanolobium*, *Dichrostachys cinerea*, and *Combretum*) using an existing natural vegetation map (developed by the University of Copenhagen's Vegetation and Climate Change in Eastern Africa project [downloaded from http://vegetationmap4africa.org/2_Vegetation_map.html]) for vegetation structure, and ground-based systematic sampling every 2 km along road transects throughout the study area for forage plants.
2. Natural predation pressure using spatial lion density data (#lions/100 km^2) and alternative prey densities (from Lee et al. 2016b = lion density/primary prey density).
3. Distance to two types of human habitation (permanent settlements and Masai bomas, mapped using Google Earth imagery).

Social covariates included:

1. Local population density of adult giraffes (#giraffes/km^2).
2. Community-level relationship strength and coefficient of variation of relationship strength (derived from social network analysis).
3. Adult female relationship strength, gregariousness, and betweenness (derived from social network analysis).

STUDY AREA

The Tarangire Ecosystem (TE) in northern Tanzania supports one of the most diverse large-mammal communities in the world, involving migrations of eastern white-bearded wildebeest, plains zebra, common eland (*Tragelaphus oryx*), fringe-eared oryx (*Oryx beisa*), Thomson's gazelle (*Eudorcas thomsonni*), and Grant's gazelle (*Nanger granti*) (Lamprey 1964, Morrison and Bolger 2014). The TE is in the eastern branch of the Great Rift Valley and encompasses roughly 30,000 km^2 (Borner 1985, Prins 1987) defined by the migratory ranges of

wildebeest and zebra from their dry-season refuge along the perennial Tarangire River north to Lake Natron and south to the Simanjiro plains and Irangi Hills (Lamprey 1964, Kahurananga and Silkiluwasha 1997, Foley and Faust 2010). Rain occurs almost exclusively in October–May, with a mean total annual rainfall of 650 mm for years 1980–2009, coefficient of variation = 42.6%, range = 312 to 1,398 mm (Foley and Faust 2010). The TE experiences three precipitation seasons per year (short rains = Oct–Jan, long rains = Feb–May, and dry = Jun–Sep). Average monthly precipitation by season were short rains = 63 mm, long rains = 100 mm, dry = 1 mm. Agriculture in the TE increased fivefold from 1984 to 2000 causing substantial habitat loss, increasing fragmentation, and reducing connectivity (Newmark 2008, Msoffe et al. 2011).

Our study area in the core of the TE is 4,400 km^2 where we sampled a 1,500 km^2 area in five administrative areas with differing management activities (Fig. 6). Land management is divided among Tarangire National Park (TNP), Lake Manyara National Park (LMNP), Manyara Ranch Conservancy (MRC), and Mtowambu (MGCA) and Lolkisale Game Controlled Areas (LGCA). The two national parks, TNP and LMNP, had high levels of wildlife protection including exclusion of livestock and human settlements and rigorous anti-poaching patrols; MRC had intermediate levels of wildlife protection with exclusion of human settlements and some anti-poaching patrols but with large numbers of livestock during the daytime. LGCA incorporated a village Wildlife Management Area with similar levels of anti-poaching efforts as MRC but with sport hunting and permanent human settlements permitted, and MGCA had no Wildlife Management Area and extensive sport hunting and permanent settlements. Legal hunting of giraffes is not permitted in Tanzania, but illegal poaching occurs. Movement analyses have determined that all administrative areas are connected by movements of adult females, albeit with only one female moving in and out of LMNP during our study period (Lee and Bolger 2017).

The Rift Valley escarpment formed the western boundary of the study area, a steep cliff that restricted giraffe movements in that direction. East of Makuyuni town along the asphalt road, wild large mammals were rarely observed due to high human and livestock population density and agriculture. West of TNP and south of LMNP was an area of high human population density and intensive agriculture. Two 2-lane asphalt roads crossed the study area.

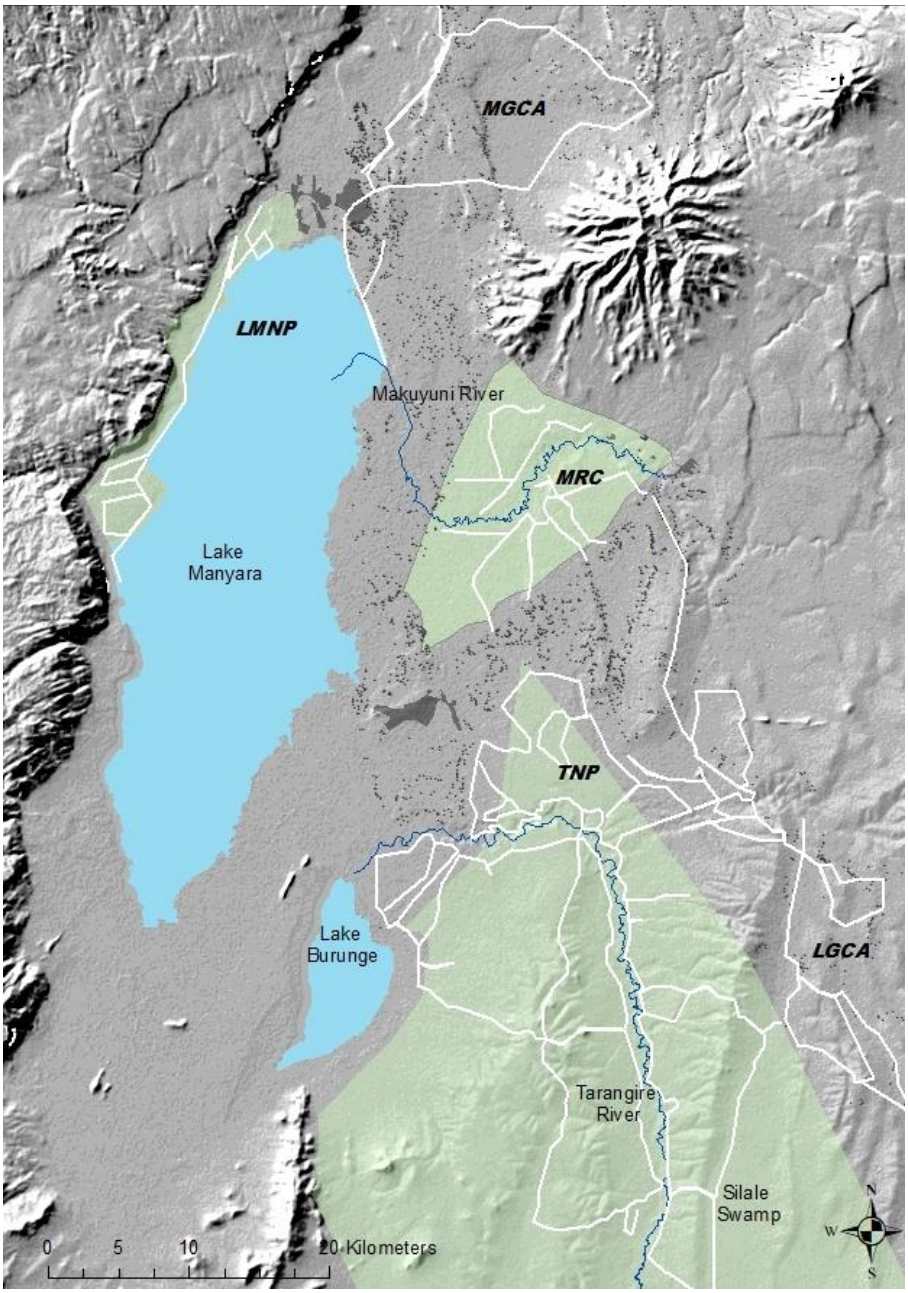

Figure 6. Study area in the Tarangire Ecosystem of northern Tanzania. White lines are tracks sampled, blue lines are rivers and watercourses, blue areas are lakes. Green polygons are protected areas. Grey points are bomas, grey polygons are towns.

CONSERVATION IMPLICATIONS

This is the largest individual-based demographic study of giraffes conducted to date, in terms of both study area and sample size, and will provide much-needed information about population dynamics of a tropical ungulate in an ecosystem affected by human uses. An intricate knowledge of social dynamics and fine-scale spatial demography in a fragmented ecosystem can help wildlife managers pinpoint and ameliorate specific factors implicated in local population declines. The giraffe can serve as an example species to investigate social and demographic responses to factors that are hypothesized to affect other tropical ungulates with fission-fusion social systems that are confronting similar threats such as predation, poaching, and natural and anthropogenic changes in vegetation. As such this study will contribute significantly to scientific understanding of the population biology of spatially and socially structured animal populations in the face of a rapidly changing planet.

Chapter 1

Fission–fusion dynamics of giraffe groups are driven by ecological, anthropogenic, temporal, and social factors

Monica L. Bond · Derek E. Lee · Arpat Ozgul · Barbara König

Published in *Oecologia* (2019) 191, 335–347. doi:10.1007/s00442-019-04485-y

Abstract Fission–fusion dynamics hypothetically enable animals to exploit dispersed and ephemeral food resources while minimizing predation risk. Disentangling factors affecting group size and composition of fission–fusion species facilitates their management and conservation. We used a 6-year dataset of 2,888 group formations of Masai giraffes in Tanzania to investigate determinants of social group size and structure. We tested whether ecological (lion density, vegetation structure, and prevalence of primary forage plants), anthropogenic (proximity to human settlements), temporal (rainy or dry season), and social (local giraffe density, adult sex ratio, and proportion of calves) factors explained variation in group size and sex- and age-class composition. Food availability rather than predation risk mediated grouping dynamics of adult giraffes, while predation risk was the most important factor influencing congregations with calves. Smallest group sizes occurred during the food-limiting dry season. Where predation risk was greatest, groups with calves were in bushlands more than in open grasslands, but the groups were smaller in size, suggesting mothers adopted a strategy of hiding calves rather than a predator-detection-and-dilution strategy. Groups with calves also were farther from towns but closer to traditional human compounds (bomas). This may be due to lower predator densities, and thus reduced calf predation risk, near bomas but higher human disturbance near towns. Sex- and age-based differences in habitat use reflected nursing mothers' need for high-quality forage while also protecting their young from predation. Our results have implications for conservation

and management of giraffes and other large-bodied, herd-forming ungulates in heterogeneous environments subject to anthropogenic threats.

Keywords fission–fusion, giraffe, *Giraffa camelopardalis*, grouping behaviour, social systems

Introduction

Many social species in taxa as diverse as primates, marine mammals, bats, birds, elephants, carnivores, and ungulates exhibit fission–fusion dynamics (Whitehead and Dufault 1999, Wittemyer et al. 2005, Smith et al. 2008), whereby group sizes fluctuate by merging of and splitting into subunits (Kummer 1971, Aureli et al. 2008). Such fission–fusion dynamics may enable grouping patterns to respond to short-term and seasonal fluctuations in food resources (Holekamp et al. 2012) or local predation risk (Thaker et al. 2010). The framework proposed by Aureli et al. (2008) to assess variation in group cohesion and membership emphasized examining variation in group size and composition, which can influence intra-group competition for food, daily travel distances, predation risk, and natal or breeding dispersal propensities, all of which might inflict energetic and fitness costs. Therefore, if we assume that individuals are behaving adaptively when forming groups (Chapman and Chapman 2000, Majolo et al. 2008, Markham et al. 2015), a fundamental question is which spatial and temporal factors mediate the size and composition of a group.

Spatial and temporal heterogeneity in food resources and predation risk can bring about group fission–fusion dynamics across space and time (Fortin et al. 2009). In a review of grouping behaviour of African antelopes in relation to their ecology, Jarman (1974) hypothesized that feeding style, dispersion of food resources, and anti-predatory strategies influence group size. The maximum group size is influenced by the dispersion of food and the feeding style (which limits the number of individuals that can feed together as a cohesive group), and the

minimum group size by anti-predator behaviour (if individuals benefit from communal defence or the dilution effect; Hamilton 1971). Subsequent studies observed that ungulates formed larger groups in open environments to avoid predation and congregated in areas with abundant high-quality food resources, but dispersed and formed smaller groups in areas of thick, dense vegetation (Pays et al. 2007, Fortin et al. 2009, Thaker et al. 2010). However, not all ungulates respond the same way to predation risk. For example, herds of red deer (elk; *Cervus elaphus*) disaggregated and moved to protective cover when wolves (*Canis lupis*) were present, possibly to reduce the likelihood of detection (Winnie and Creel 2007), but a recent study of two enclosed populations of Rothschild's giraffes (*Giraffa camelopardalis rothschildi*) did not find evidence that grouping is an anti-predator behaviour in the presence of lions (*Panthera leo*: Muller et al. 2018). Group composition also varies spatiotemporally, with some degree of sexual segregation in feeding behaviour and habitat use evident in many ungulate species (Clutton-Brock et al. 1987, Winnie and Creel 2007, Thaker et al. 2010).

To determine the importance of access to food and risk of predation on group size and composition would entail manipulating these factors independently of each other. Such experiments are not easily conducted on wild populations of ungulates, but observational studies in heterogeneous landscapes where free-ranging animals are exposed to varying levels of predation and a diversity of vegetation can contribute to disentangling the factors affecting group size and composition.

Like many ungulate species, the social system of giraffes exhibits fission–fusion dynamics (Dagg and Foster 1976, Leuthold 1979, Bercovitch and Berry 2012). The size and composition of both male and female groups are fluid (Dagg and Foster 1976, Leuthold 1979, Le Pendu et al. 2000, van der Jeugd and Prins 2000, Muller et al. 2018), but females form longer-term associations with other females (Pratt and Anderson 1985, Carter et al. 2013, VanderWaal

et al. 2014). Giraffe group sizes varied from one to 175 (Dagg and Foster 1976, Muller et al. 2018). Subadult males form bachelor herds in which they establish dominance hierarchies and adult males range widely seeking adult females in oestrus (Pratt and Anderson 1985). Females are receptive at any time of year (Dagg 2014).

Giraffes are non-territorial, resident browsers that feed mostly on leaves, twigs, flowers, and fruits of *Acacia* spp., *Dichrostachys cinerea*, and other woody plants (see references in Dagg 2014), with preference for certain species depending on season and vegetation type, and with differences between males and females in vegetation consumed (Pellew 1984, Caister et al. 2003, Mramba et al. 2017). Giraffes occur in various habitat types from dense woodland to savanna grasslands (Dagg and Foster 1976, Leuthold 1979), and many giraffe populations roam over increasingly fragmented landscapes affected by human uses (Lee et al. 2016a, Lee and Bolger 2017). Previous studies observed that adult males were located more often in closed habitats than females (Leuthold 1979, Mramba et al. 2017). Adult females with calves formed smaller groups than those without calves (Muller et al. 2018) and tended to feed in open areas seasonally (Ginnett and Demment 1999), while pregnant females were found in densely vegetated habitats, which might be either an anti-predator strategy to hide neonatal calves or selective foraging to decrease tannin intake (Young and Isbell 1991, Furstenburg and van Hoven 1994, Caister et al. 2003). Therefore vegetation type, season, and presence of calves are expected to influence habitat use and group dynamics.

Our objective was to investigate how spatial, temporal, and social factors influence the dynamics of Masai giraffe (*G. c. tippelskirchii*) grouping behaviour in a large (N > 3,100 individuals) free-ranging metapopulation studied over 6 years. Animals were individually identified using photographic capture-recapture methods. We modelled effects of ecological (lion density, vegetation structure, and prevalence of primary forage plants), anthropogenic

(proximity to human settlements), temporal (rainy or dry season and time of day), and social factors (local giraffe density, adult sex ratio, and proportion of calves) on group size and composition. Given the giraffe's fission–fusion social system and tendency to range widely in temporally and spatially heterogeneous environments, we expected to gain a general understanding of the relative influence of food availability and predation risk on grouping behaviour of this megaherbivore by testing the following hypotheses related to the costs and benefits of group living in ungulates.

If grouping behaviour is predominantly affected by feeding competition, we predicted smaller groups during the season of low food availability, as well as in areas with lower availability of preferred food. Predation may counteract the benefits of small groups under competitive feeding conditions if the dilution effect is important (Hamilton 1971). If this is the case, we predicted that in places or times with low primary forage availability larger groups will form in areas with higher lion densities than in areas with lower lion densities. Differences among individuals in age and breeding status will result in modifications of group composition when trading off between the benefits of food availability and the costs of predation (Ruckstuhl 2007). Giraffe calves are the age class most vulnerable to predation (Strauss and Packer 2013), thus we predicted that adult females with calves aggregate in larger groups in areas with high lion densities and/or low vegetation cover than females without calves, according to the predator-detection (Pulliam 1973) and dilution-effect hypotheses (Hamilton 1971). As one of the world's few extant megaherbivore species, constituting an extreme along the life-history spectrum, studies of giraffes can elucidate the general applicability of patterns observed in studies of smaller-bodied species by providing an allometric endpoint for comparison and contrast (Owen-Smith 1988).

Methods

STUDY AREA

Our study area in the Tarangire Ecosystem (TE) of northern Tanzania included a heterogeneous savanna landscape inside and outside protected areas, with unprotected lands experiencing rapid fragmentation due to human use (Morrison and Bolger 2014) and illegal killing of giraffes for meat affecting adult female survival in some subpopulations (Lee et al. 2016a). Our study area was unfenced and individuals moved throughout the area, including crossing tarmac roads and agricultural areas between habitat patches (Lee and Bolger 2017). They could access a diversity of vegetation types at varying distances from human habitation. Protected areas supported a higher density of predators such as lions and spotted hyenas (*Crocuta crocuta*) compared to unprotected lands, so the giraffes also experienced various levels of natural predation (Lee et al 2016a,b).

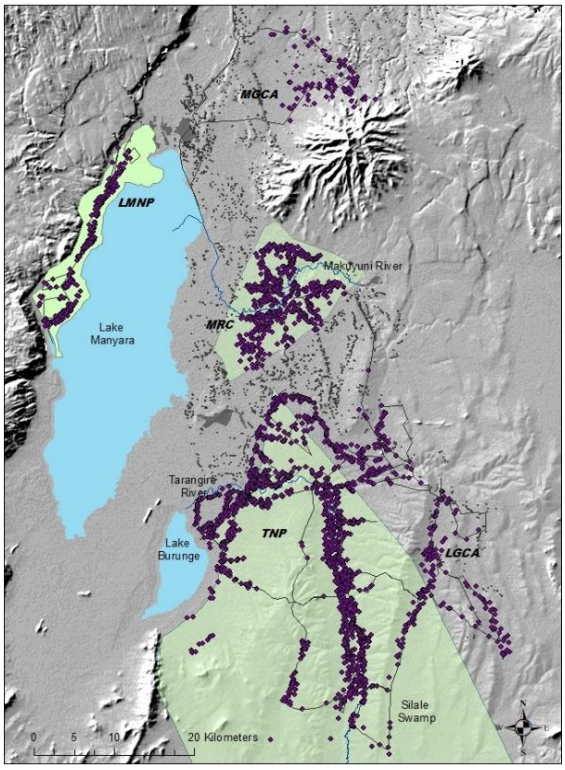

Figure 1. Location of 2,888 Masai giraffe group formations (purple dots) in the Tarangire Ecosystem of northern Tanzania, 2011–2016. Dark grey lines are roads and tracks surveyed for giraffe groups, blue lines are rivers, light blue areas are alkaline, green areas are national parks and conservancies lakes, grey polygons are towns and grey points are bomas. LMNP = Lake Manyara National Park, TNP = Tarangire National Park, MRC = Manyara Ranch Conservancy, MGCA = Mtowambu Game Controlled Area, and LGCA = Lolkisale Game Controlled Area.

The TE supports one of the most diverse large-mammal communities in the world (Lamprey 1963). The TE is situated in the eastern branch of the Great Rift Valley and encompasses roughly 30,000 km^2 (Borner 1985, Prins 1987). Rain occurs almost exclusively from October–May, with a mean total annual rainfall of 650 mm for the years 1980–2009 (coefficient of variation = 42.6%, range = 312 to 1,398 mm; Foley and Faust 2010). The TE

experiences three precipitation seasons per year (short rains = Oct–Jan, long rains = Feb–May, and dry = Jun–Sep), with respective average monthly precipitations of 63 mm, 100 mm, and 1 mm. Human population and agricultural development in the TE have increased with 3% annual human population growth between 2003 and 2012, adding nearly 800,000 people (TNBS 2013), causing substantial habitat loss, increasing fragmentation, and reducing connectivity for wildlife (Msoffe et al. 2011, Morrison and Bolger 2014).

Our study area in the core of the TE was 4,400 km^2 within which we sampled a 1,500-km^2 area with differing management activities (Fig. 1). Land management was divided among five administrative sections: (1) Tarangire National Park (TNP), (2) Lake Manyara National Park (LMNP), (3) Manyara Ranch Conservancy (MRC), and (4) Mtowambu (MGCA) and (5) Lolkisale (LGCA) Game Controlled Areas. The two national parks, TNP and LMNP, had high levels of wildlife protection including exclusion of livestock and human settlements and rigorous anti-poaching patrols. MRC had intermediate levels of wildlife protection with exclusion of human settlements and some anti-poaching patrols but with large numbers of livestock during the daytime. LGCA and MGCA had the lowest levels of wildlife protection and allowed sport hunting and permanent human settlements. None of the administrative areas were fenced, and all were connected by movements of adult female giraffes (Lee and Bolger 2017), thus we considered our study population to be a metapopulation of subpopulations connected through dispersal.

The western boundary of the study area was formed by the Rift Valley escarpment, a steep cliff that restricted giraffe movements in that direction. Wild large mammals were rarely observed due to high human and livestock population densities and intensive agriculture east of Makuyuni town, west of TNP, and south of LMNP. Two 2-lane asphalt roads crossed the study area (Fig. 1).

DATA COLLECTION

Giraffes are relatively conspicuous and easily approached (Pratt and Anderson 1985). They have unique markings that do not change from birth to death (Foster 1966), enabling all or most group members to be identified using non-invasive photographic capture-recapture techniques. We conducted 31 daytime, fixed-route dirt track transect surveys for giraffe groups between May 2011 and October 2016. We surveyed on three primary sampling periods per year near the end of each precipitation season (short rains=Jan, long rains=May, and dry=Sep) according to a robust design with each primary sampling period composed of two independent, back-to-back secondary sampling periods during which all fixed-route dirt track transects in the study area were surveyed (Pollock 1982). In 2011, surveys were part of a pilot study and were conducted only during the long rainy season. Surveys were conducted between 0700 and 1800 h, beginning approximately 0.5 h after sunrise and ending 0.5 h before sunset. Driving speed was maintained between 15 and 20 km/h on all transects, and all survey teams included the same two dedicated observers and a driver. Each survey took 7–10 days, and each road segment was sampled only once in a given secondary sampling period. The minimum number of days that passed before the same track was re-sampled was 5 days, thus enabling giraffes to re-group and ensuring independence of the sampling events.

When we encountered a giraffe group we approached to within at least 150 m for data collection. We defined a group as one or more giraffes foraging or moving together, but not moving past each other in opposite directions, and that was >500 m from the next nearest giraffe, which we considered to be a separate group. Giraffe groups were usually self-defining as the distances between individuals were substantially less within than between groups. Individuals with no conspecific within 500 m were considered singletons. We recorded the following data for each individual: age class (calf, subadult, adult), sex, date, time of day, and GPS location for

the approximate centre of the group. We used a suite of physical characteristics, including body shape, height, relative length of the neck and legs, and ossicone characteristics to categorize giraffe into the three age classes: calf (<1 year), subadult (1–3 years), or adult (>3 years), based on Strauss et al. (2015).

We 'captured' or 'recaptured' every individual by photographing them on the right side and using Wild-ID software to match photos of individuals based on their unique spot patterns (Bolger et al. 2012). We typically photographed and identified every individual in every group we encountered although rarely we missed some individuals due to difficult terrain or the animals departing before photo-capture. When this occurred, we noted the number of animals we knowingly failed to photograph; overall we missed one or more individuals in 1.7% of the groups we encountered each year. Therefore we are confident that our counts were a robust index of actual groups in our study area. Our study design involved repeatedly measuring individually identified giraffes, with each individual assigned to only one group per primary sampling period, but with the same or a different set of individuals in groups during subsequent primary sampling periods. We used these individual-based data to calculate group size and composition.

ENVIRONMENTAL, TEMPORAL, AND SOCIAL COVARIATES

We plotted group locations on a GIS using ArcMap 10.5.1 (Environmental Systems Research Institute, Redlands, CA, USA), and at every location, we extracted the environmental and anthropogenic variables of vegetation type and proximity to nearest human settlements (permanent towns and traditional non-permanent family compounds known as bomas). We used a combination of publicly available remote-sensed data and our own ground-based vegetation surveys to create GIS vegetation features. These features included four general vegetation types from most dense to most open to represent structure and cover: (1) deciduous bushland and

thicket, (2) wooded grassland, (3) edaphic grassland on volcanic soils with scattered woody species, and (4) edaphic grassland on drainage-impeded or seasonally flooded soils (Kindt et al. 2011), derived from a natural vegetation map developed by the University of Copenhagen's Vegetation and Climate Change in Eastern Africa (VECEA) project (downloaded from http://vegetationmap4africa.org/2_Vegetation_map.html). Within each general vegetation type we used ground-based observations collected in 2014 every 2 km along our dirt tracks to map polygons of specific vegetation types of large stands with >10% cover of one of four primary giraffe forage species: (1) *Acacia tortilis*, (2) *Acacia drepanolobium*, (3) *Dichrostachys cinerea* and (4) *Combretum* (Foster 1966, Pellew 1984, Young and Isbell 1991, Furstenburg and van Hoven 1994, Caister et al. 2003). In our analysis of specific primary forage types, we classified locations with <10% cover of any of the four forage species as non-specific. We used Google Earth imagery to map bomas as points and permanent towns as polygons. To calculate distances to bomas we used the Point Distance proximity function and to calculate distances to towns we used the Near proximity function in ArcMap.

We obtained data on lion densities in each administrative unit from Lee et al. (2016b). Lions were surveyed from 2010–2013 by the Tarangire Lion Project and Lake Manyara National Park staff, and site-specific lion densities per 100 km^2 were calculated by dividing lion population size in each administrative unit averaged across all seasons, by the area enclosed by a minimum convex polygon of our surveyed road network in each unit (Lee et al. 2016a). TNP, LMNP, and MRC had higher lion densities due to active predator protection (8.6, 20.5, and 14 lions/100 km^2, respectively), whereas trophy hunting of lions and pastoralist activities in the two GCA sites resulted in lower lion densities there (1.7 lions/100 km^2).

Group sizes of ungulates increase with population density (Pépin and Gerard 2008), thus we explicitly accounted for local giraffe population density. We calculated giraffe density in

each of the five administrative areas and assumed that it did not substantially change over the study period (see Lee et al. 2016a). Density was adult $\widehat{N}$ / surveyed area (km^2) of each administrative area, with surveyed area calculated as the minimum convex polygon enclosing our dirt track network in each area, plus a boundary strip equal to half the width of the estimated mean maximum distance moved (Parmenter et al. 2003).

STATISTICAL ANALYSIS

We quantified group size and composition by age-class and sex for every observed group, and investigated how environmental, seasonal, and social factors influenced (1) group size (number of individuals); (2) proportion of calves in a group; and (3) probability of being a single adult male, single adult female, bachelor herd, mixed-sex group without calves, or any group with one or more calves (group type). We considered groups with both $\geq$2 individuals and $\geq$0.5 proportion of adult and/or subadult males to be bachelor herds. Each individual was assigned to only one group per survey (31 surveys) but had the potential to be observed with a different or the same set of individuals during other surveys, thus the study design consisted of repeated measures of individual giraffes.

We assessed multicollinearity among the predictor variables by computing the variance inflation factor using the vif function in package car for R version 3.4.3 (R Core Team 2017). We fitted generalized linear mixed models (GLMMs) utilizing a Markov chain Monte Carlo (MCMC) approach in a Bayesian statistical framework (Ellison 1996) with package MCMCglmm (Hadfield 2010). We used a zero-truncated Poisson distribution for our group size response variable, to account for the impossibility of a group size of zero, and used the canonical log link function to model group size as a linear combination of our predictors. We conducted binomial regression with the logit link function and a binomial distribution to model proportion

of calves in a group, and multinomial regression with the canonical logit link function and a categorical distribution to model group type as responses to predictors. We modelled environmental, seasonal, and social predictors as fixed effects, group ID as a random predictor to account for non-independence of individuals within a group, and a vector of residuals to account for overdispersion in our data with a "unit-level" random effect for each observation (Hadfield 2010). All models were run for 100,000 iterations with a burn-in phase of 5,000 and thin interval of 100. We examined trace plots and posterior density estimates of variance components, as well as effective sample sizes, to assess model convergence. We attempted to model both group ID and individual ID as random effects together, but this model suffered from singularity where the variance of individual ID was estimated as zero, likely due to large numbers of singletons and individuals seen only once. Increasing the iterations and burn-in period failed to rectify the singularity, so we modelled only group ID as a random effect.

We accepted fixed effects as significant when their 95% credible intervals did not span zero, and the group ID random effect as significant when the distribution was not close to zero (Hadfield 2010). For interpretation we exponentiated the coefficients from the Poisson regression models and calculated the inverse-logit of the coefficients from multinomial and binomial regression models. Details about variables, models tested, and priors and variances selected are available in Supplementary Materials.

Results

During our study period (2011–2016) we encountered a total of 2,888 giraffe group formations, comprised of 3,117 uniquely identified individuals. Of these individuals 1,859 were adults when first entered into our database (1,139 females and 720 males). Groups on average comprised 5.4 giraffes (SE = 0.11; range 1–66), and the most frequent (modal) group size was 1 (Fig. 2). Groups of ≥2 individuals averaged 6.9 giraffes (SE = 0.15; range 2–66). Of the adult singletons, 401 (61%) were males and 259 (39%) were females. We recorded 321 bachelor herd formations, comprised of 2 or more individuals with a proportion of adult and subadult males ≥0.5 (mean group size: 8.3 ± 0.53). One or more calves were detected in 753 group formations (mean group size: 9.1 ± 0.33). The remainder of group formations (1,180) were mixed-sex, female-dominated herds with no calves (mean group size: 5.1 ± 0.15).

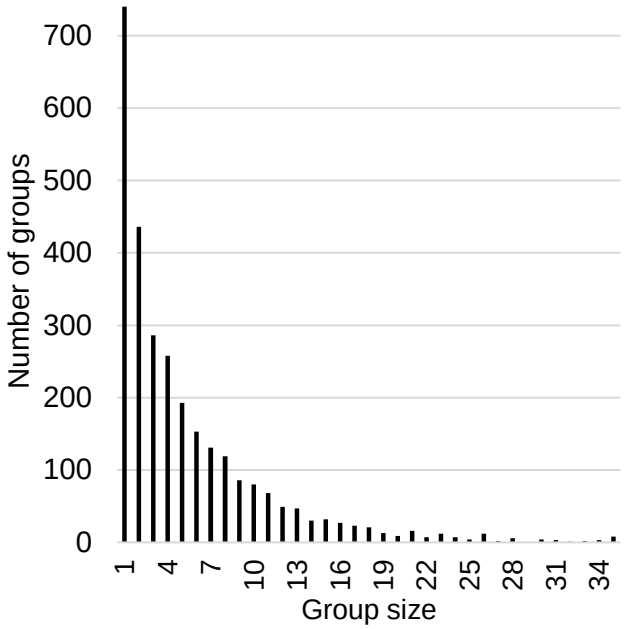

Figure 2. Number of giraffe group formations (N = 2,888) by size over 6 years (2011–2016).

Concerning the specific primary forage types where giraffes were encountered, 1,375 groups (48%) occurred in *A. tortilis*. We recorded 337 groups (12%) in *D. cinerea*, 320 (11%) in *A. drepanolobium*, 62 (2%) in *Combretum*, and 794 (27%) located in stands not dominated by any of these four types (non-specific). Five of the six largest groups, ranging in size from 40 to 66 individuals, occurred in extensive patches of *D. cinerea* on the western side of MRC during the long rains (4 groups) or short rains (1 group).

Assessments of variance inflation factors indicated low collinearity among explanatory variables. Visual inspection of trace plots for sampled posteriors and graphs of density estimates indicated good mixing of all the models.

FACTORS AFFECTING GROUP SIZE

Significant effects for giraffe group size included: proportion of adult males, time of day, season, a season × specific primary forage type interaction, and a lion density × general vegetation × proportion of calves interaction (Table 1). Distance to bomas and towns and local giraffe population density did not significantly affect group sizes. Posterior mean parameter estimates and 95% upper and lower credible intervals for all predictor variables in the global model are presented in Supplementary Materials Table S1.

Groups increased in size over the course of the day but tapered off late in the afternoon, in a quadratic relationship with hour (Fig. 3). Group sizes were significantly influenced by season and the interaction between season and specific primary forage type.

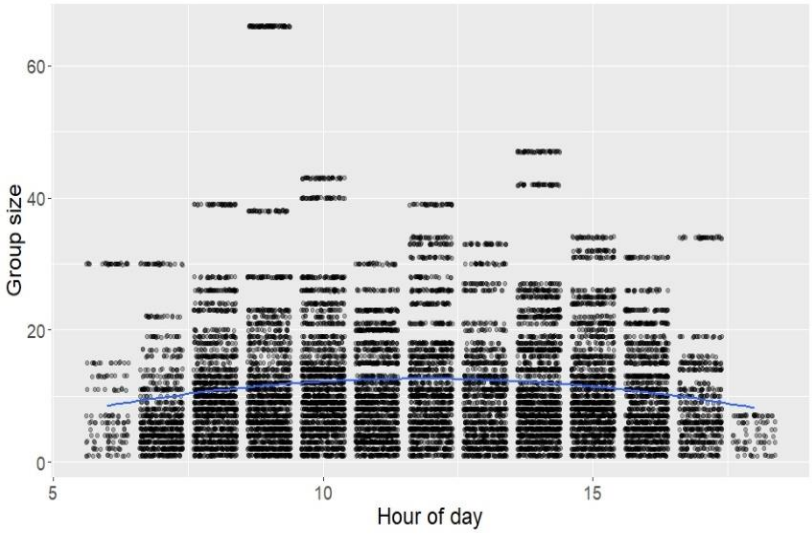

Figure 3. Giraffe group sizes throughout the course of a day.

Food availability is expected to be lower thus competition over food greater in the dry season, and giraffe groups were 30% smaller in the dry than the rainy seasons. When compared to non-specific primary forage patches during the long rainy season, groups in areas with large stands of

Combretum were larger in both the dry (~ 313%) and short rainy season (~ 221%), although very few groups were found in *Combretum* overall (2%).

Group size was affected by a significant lion density × general vegetation × proportion of calves interaction. The more calves (in relation to adults) a group had, the smaller it was in dense vegetation in areas with higher lion densities (Fig. 4). Overall, smaller groups had higher proportions of adult males.

Table 1. Posterior mean values of significant fixed effects, 95% credible intervals, and probability of significance for determinants of group size (N=2,888 groups), proportion of calves in a group, and type of group for Masai giraffes (*Giraffa camelopardalis tippelskirchii*) in the Tarangire Ecosystem, northern Tanzania, 2011–2016. Estimates from generalized linear mixed regression models run for 100,000 iterations with a burn-in phase of 5,000 and thin interval of 100. Group identification was considered a random effect to account for non-independence of group members. Descriptions of models and results of all effects presented in Table S1, Supplementary Materials.

Variable[a]	Posterior Mean of ß Estimate	Lower 95% CI	Upper 95% CI	pMCMC
Group Size				
Dry	-0.362	-0.650	-0.102	0.021
Hour	0.300	0.189	0.416	< 0.001
$hour^2$	-0.011	-0.016	-0.007	< 0.001
asin(P_AM)	-0.623	-0.703	-0.534	< 0.001
dry:SPVEGcomb	1.144	0.291	2.013	0.006
shortr:SPVEGcomb	0.793	-0.014	1.553	0.040
LION:asin(P_C):GENVEGbd	-0.105	-0.179	-0.019	0.017
Proportion Calves				
D_Boma	-0.043	-0.064	-0.023	< 0.001
SPVEGadrep	0.310	0.018	0.570	0.040
Group Composition				
traitTYPE.BACH:D_Boma	0.230	0.120	0.360	< 0.001
traitTYPE.CALF:D_Boma	-0.190	-0.310	-0.080	< 0.001
traitTYPE.SM:D_Boma	0.060	0.020	0.100	< 0.001
traitTYPE.CALF:D.Town	0.050	0.010	0.090	0.034
traitTYPE.SF:SPVEGdichro	-3.890	-7.060	-0.200	0.027
traitTYPE.BACH:GENVEGbd	-2.720	-4.450	-1.630	< 0.001
traitTYPE.CALF:GENVEGbd	2.070	0.950	3.220	< 0.001
traitTYPE.SF:GENVEGbd	-0.510	-1.110	-0.050	0.046
traitTYPE.SM:GENVEGbd	-0.790	-1.290	-0.250	< 0.001
traitTYPE.CALF:GENVEGg	2.410	0.000	5.160	0.042
traitTYPE.CALF:GENVEGgv	2.560	1.160	4.200	< 0.001

traitTYPE.SF:SPVEGdichro:SEASONdry	6.530	0.770	11.520	0.004
traitTYPE.CALF:SPVEGadrep:SEASONshortr	10.340	1.630	18.650	0.006
traitTYPE.SF:SPVEGadrep:SEASONshortr	5.900	0.610	11.490	0.011
traitTYPE.SF:SPVEGcomb:SEASONshortr	5.950	0.890	10.850	0.029

[a] LION=local lion density in 5 administrative sites Tarangire and Lake Manyara National Parks, Manyara Ranch Conservancy, Mtowambu and Lolkisale Game Controlled Areas (#lions/100 km^2); Season: dry (Sep-Oct), shortr (short rains, Jan-Feb) as compared with reference category long rains (May-Jun); Time of day (hour); P_AM=adult males/adult males+adult females; P_C=number of calves/number of individuals in group (proportions arcsin-transformed); D_Boma=distance (km) to nearest boma (Masai family compound) D_Town=distance (km) to permanent town; General vegetation type (GENVEG): bd (deciduous bushland and thicket), g (grassland on flooded soils), gv (grassland on volcanic soils) as compared with reference category wd (wooded grassland); Specific primary forage type (SPVEG): dichro (*Dichrostachys cinerea*), comb (*Combretum spp.*), adrep (*Acacia drepanolobium*), and atort (*Acacia tortilis*) compared with reference category nonspecific (NONSP); traitTYPE=bachelor herd (BACH), single male (SM), single female (SF), female-dominated mixed group without calves (MIXED), and female group with calves (CALF).

FACTORS AFFECTING GROUP COMPOSITION

The proportion of calves in a group varied by distance to bomas and specific primary forage type, but not by general vegetation, lion density, season, or distance to towns (Table 1, Supplementary Materials Table S2). Groups closer to bomas had a higher proportion of calves (the proportion of calves decreased by 51% with each kilometre away from the nearest boma). The proportion of calves also varied by specific primary forage type, with 58% more calves in groups in *A. drepanolobium* than in non-specific primary forage types.

Group types were differently influenced by vegetation, season, and anthropogenic land use as well as season × vegetation interaction (Table 1, Supplementary Materials Table S3). The further away from a boma, the higher was the probability that the group was a bachelor herd or a single adult male. For every kilometre increase away from a boma, the predicted odds of a group being a bachelor herd increased by 56% and the odds of being a single male increased by 52%. Conversely, the closer to a boma we observed a group, the higher was the probability of being a calf group, and with every kilometre increase away from a boma the odds of being a calf group decreased by 55%. Calf groups also significantly avoided towns, being 51% more likely for each kilometre increase away.

Calf groups were most likely to be observed in deciduous bushlands and thickets than in open wooded grasslands (by 88%), whereas bachelor herds (94%), single males (69%), and single females (63%) were less likely to occur there. Calf groups were also more likely to occur in grasslands on volcanic soils (by 92%) and seasonally flooded grasslands (93%) than in open wooded grasslands.

Prevalence of primary forage plants affected the probability of encountering a single female or a calf group. Compared with non-specific primary forage types, single females were 99% more likely to be observed in areas dominated by *D. cinerea* during the dry than rainy seasons. During the short rains, they were more often seen in *Combretum* (100% more likely) and in *A. drepanolobium* (99% more likely). Calf groups also were 100% more likely in *A. drepanolobium* during the short rains.

Vegetation type (either general or specific) or anthropogenic land use did not affect the probability of observing a mixed-sex group without calves.

Discussion

Our 6-year study of 2,888 Masai giraffe group formations in the Tarangire Ecosystem found food availability was more important than predation risk in mediating grouping dynamics of adult giraffes. Predation risk, on the other hand, was a significant predictor of where groups with calves congregated. Where natural predation risk was high, adult females with dependent calves tended to form smaller groups, and to seek cover in thicker vegetation. Calf groups also tended to be found closer to traditional pastoralist homesteads (bomas) where behaviours of predators are disrupted, but avoided towns which had high human populations, agriculture, and poaching risk. Giraffe groups closer to bomas also had higher proportions of calves. Conversely, male groups roamed farther from traditional homesteads. Single females (possibly pre- or post-

partum) and females with calves (calf groups) exhibited more seasonal selectivity of primary forage plants than other group types, possibly due to strict nutritional requirements.

Overall giraffe group size distribution and compositions were approximately similar to those previously reported in the Tarangire Ecosystem and elsewhere in the species' range. Single individuals were the most frequently encountered 'group size', and on average groups comprised five to six individuals (Leuthold 1979, Le Pendu 2000, van der Jeugd and Prins 2000, Bercovitch and Berry 2009, Shorrocks and Croft 2009, VanderWaal et al. 2014, Wolf et al. 2018, Muller et al. 2018). Interestingly, we found that time of day influenced fission–fusion dynamics, with giraffe groups starting out smaller in the morning and growing larger (fusing) over the course of the day to a mid-afternoon maximum and then fissioning again towards the evening. Giraffes may aggregate during the day for foraging, possibly attracted to a patch due to the presence of conspecifics (Stutz et al. 2018). Females may also use fusion events to aggregate with kin, as adult females with closer social ties tended to be more related to each other than random (Carter et al. 2013).

GROUP SIZE MODIFIED BY COMPETITION OVER FOOD

Consistent with our predictions, giraffe groups were largest in the wet seasons, potentially due to an abundance of quality food resources reducing intra-group competition (Leuthold 1979, Le Pendu et al. 2000, Bercovitch and Berry 2009). Tropical zones show seasonal peaks in herbivore food supply and quality driven by the onset of seasonal rainfall (Rubanza et al. 2005, Ogutu et al. 2007). Woody browse plants in the African savanna begin growing at the start of the rains and continue to produce new foliage throughout their photosynthetically active season (Jarman 1974). Large herbivores track fluctuations in plant phenology by moving to areas where their forage is at its peak nutritional quality (Pellew 1984,

Frank and McNaughton 1992, Wang et al. 2006). In our study area giraffe group sizes were largest overall in the short rains, right after the vegetation first flushes, leading to feeding congregations. Though *D. cinerea* did not significantly affect group size in our analysis, we observed the largest giraffe groups in this specific forage type during the rainy seasons, suggesting this bush was a seasonally important food source. *Combretum* may also be seasonally important as group sizes in patches dominated by this primary forage type were larger in the dry season and short rains, but very few giraffe groups overall were detected in *Combretum* so further study is warranted. Giraffes likely disperse into smaller groups over the landscape to reduce competition for browse during the dry season when food is most limiting. This seasonal grouping behaviour is similar to that of another savanna megaherbivore, the African elephant (*Loxodonta africana*) in which large aggregations are observed at the onset of the rains and group sizes dwindle as the dry season progresses (Leuthold 1976, Western and Lindsay 1984, McKnight 2015).

Giraffe group sizes in general were not larger in areas with high lion densities, neither during the food-limiting dry season nor in areas with lower prevalence of primary forage plants. Groups also were not larger in dense bushlands and thickets or in the most open vegetation. These results indicate that giraffes do not pursue an anti-predator strategy via the detection- or dilution-effect as we predicted. This is in contrast to previous hypotheses regarding this species (Bercovitch and Berry 2009) and other savanna ungulates such as wildebeests and zebras (Thaker et al 2010). The fact that giraffe groups were smaller in the early morning and evening when natural predators are most active further refutes the detection or dilution hypotheses and provides support for the importance of food availability and feeding competition in mediating group sizes overall. Lions prefer to hunt not only after daylight but in good cover (Hopcraft et al. 2005), yet we found no support for an interaction between hour of day and vegetation structure.

Thus giraffe groups neither fuse nor fission in dense compared with open vegetation in the evening, indicating that predation risk did not strongly affect overall grouping behaviour (with the exception of adult females with calves; see below). This agrees with observations on two smaller, enclosed Rothschild's giraffe populations in Kenya (Muller et al. 2018). Our study, however, goes beyond previous studies in that it encompassed a large population of giraffes of all age classes observed over six years in various seasons, roaming over a variety of habitat types including lands occupied by people.

SPECIAL REQUIREMENTS OF CALVES

Natural predation will not likely influence grouping behaviour for adult giraffes, as few adults are taken by lions (Strauss and Packer 2013). However, we found predation risk did influence grouping behaviour of adult females with dependent calves. Groups with a greater proportion of calves were smaller in areas with higher densities of lions and in dense bushlands and thickets. This suggests that mothers adopt a hiding strategy for calves, utilizing the protection of bushlands and thickets and congregating in smaller groups to avoid being detected by predators, rather than congregating in open areas according to the predator detection or dilution hypotheses. Proportion of calves in groups was also higher in

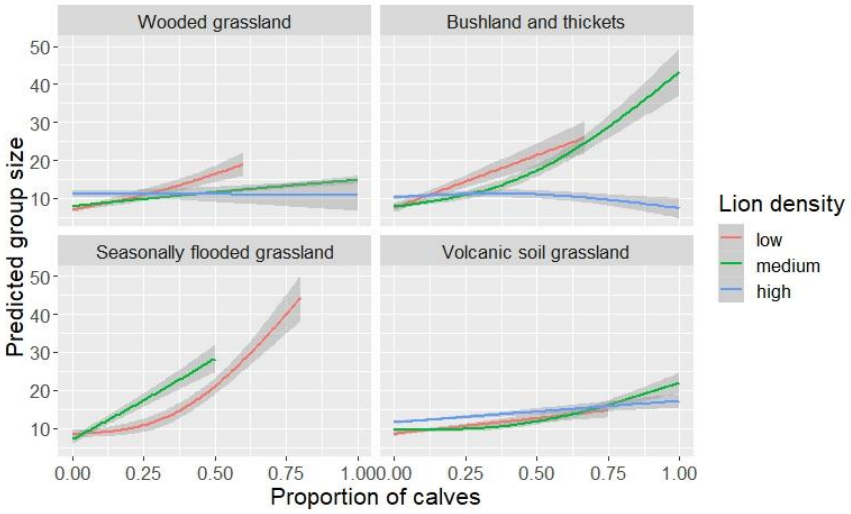

Figure 4. Effect of interaction among proportion of calves, lion density, and vegetation structure on predicted giraffe group size. Interaction effect was significant only in bushland and thicket vegetation type, where group size decreased with greater proportion of calves as lion density increased.

areas closer to traditional Masai bomas where humans disrupt predator behaviour (Kissui 2008, Mogensen et al. 2011). We speculate that calves gain protection by grouping in smaller numbers in the presence of predators, hiding in dense vegetation, and aggregating in larger numbers in areas with lower natural predator densities such as near traditional Masai bomas. Calf groups also may gain protection by avoiding areas of intensive human disturbance.

We found evidence of segregation in habitat use, whereby groups with calves were more likely to occur in dense bushlands and thickets while bachelor herds as well as single males and single females avoided these vegetation types. Calf groups were also more likely to occur in *A. drepanolobium* during the short rains, and single females (possibly pre-partum or nursing a concealed neonatal calf) preferred both *A. drepanolobium* and *Combretum* in the short rains, whereas no other group types were influenced by primary forage type. Therefore habitat choices by nursing mothers are constrained by both the need to protect their young calves from predators and the high energetic demands of lactation (Pellew 1984).

Lions are most likely to hunt in areas of good cover, thus denser vegetation poses a predation risk, yet neonatal giraffe calves hide in thick bushes during the first few weeks of life (Langman 1977). Our results contrasted with two previous studies of giraffes (Young and Isbell 1991, Ginnett and Demment 1999), which found that females with young preferred open habitats with potentially better views of predators. Giraffe calves form crèches accompanied by one or a few older females, so mothers can range relatively far from their offspring to drink or forage (Dagg and Foster 1976, Leuthold 1979). The formation of these crèches may be an effective solution to the problem of balancing predation risk on young calves with nutritional requirements of mothers (Young and Isbell 1991). With the crèche system it could be feasible for mothers to forage in denser vegetation and leave their calves in open areas where lions are less likely to hunt or more likely to be seen. However, calf groups were more likely in the bushlands and thickets,

though they congregated there in smaller numbers in areas with higher lion densities. We conclude that dense thickets not only support high-quality forage for giraffe mothers, but also provide protective and camouflaging structure for the calves to hide from predators. Giraffes at their most vulnerable age appear to be behaviourally similar to browsing Tragelaphine and smaller-bodied antelopes of sub-Saharan Africa, which also prefer dense bushes as concealment from predators (Estes 1991).

Groups with calves were encountered most often in *A. drepanolobium* during the short rains, and had proportionally more calves, potentially indicating high nutrient quality among the four primary forage plants. This corroborates previous studies that found adult female giraffes heavily utilized *A. drepanolobium*, particularly females with young (Young and Isabel 1991) and during the wet season (Mramba et al. 2017). Kindt et al. (2011) noted that wooded grassland dominated by gall *Acacias* in eastern Africa usually form an ecotone between deciduous bushland thickets and drainage-impeded open grasslands that retain water. The importance of both deciduous bushlands and *A. drepanolobium* for calf groups might be explained by the fact that these vegetation types typically occur in close proximity, thus providing protective structural cover for calves to hide from predators while also containing forage plants that satisfy the nutritional needs of lactating mothers and being located near to drinking water.

Still, giraffe calves in our study were not found exclusively in the denser vegetation. Calf groups were more likely to occur in both volcanic soil grasslands and in seasonally flooded grasslands than in wooded grasslands. Volcanic soils are especially fertile, which may enhance forage quality (Hansen et al. 1985), and seasonally flooded grasslands are often near *A. drepanolobium*, lending support for the idea that female groups with calves select habitat based on their nutrient requirements. However, these grasslands are also more open, which supports the predator-detection or dilution hypotheses. It is possible that there is a disparity in habitat use

between neonates and older giraffe calves, with neonates more likely to hide in denser vegetation and older calves found in more open areas to avoid or better escape predators when they are detected. We did not differentiate between neonates and older calves in this study, and further research accounting for the ages of calves might shed additional light on the predator detection versus hiding strategies of juvenile giraffes.

As East African savanna landscapes grow increasingly dominated by human uses (Msoffe et al. 2011), it is critical to understand grouping behaviours of giraffes in relation to anthropogenic factors. Adult females with calves were more likely to be located closer to traditional family compounds, and groups there contained a higher proportion of calves, while the reverse was true for single adult males and bachelor herds. This result likely reflected lower predator densities near bomas which reduced calf predation risk, as humans often kill lions and other carnivores in retaliation for livestock depredation (Kissui 2008) or disrupt predator behaviour (Mogensen et al. 2011). Conversely, calf groups had a lower probability of being close to towns, suggesting a difference in preference between traditional bomas versus more densely populated human settlements.

CONCLUSIONS FOR CONSERVATION

We used the heterogeneity of our unfenced landscape-scale study area, where a large population of free-ranging giraffes were exposed to varying levels of natural predation and human disturbance and a diversity of vegetation over many seasons, to disentangle the relative influence of food availability versus predation risk and anthropogenic disturbance on grouping behaviour of a megaherbivore. Our study documented the complex interplay between group size and composition, vegetation and predation risk, and human settlements. In contrast to previous studies we found groups with calves were more likely to be found in the densest vegetation,

supporting the hypothesis that deciduous bushlands serve a protective role and are important for giraffe reproduction. Additionally, areas near bomas may provide refuge for calves, possibly by lowering natural predation risk, indicating that traditional human settlements are compatible with persistence of giraffe populations, whereas intensive human disturbance in and around towns likely represents a threat. Future studies examining the fitness consequences of grouping and other social behaviours in heterogeneous environments would improve our understanding of the effects of socioecological factors on population dynamics and persistence.

Supplementary Materials

VARIABLES, MODELS TESTED, AND PRIORS AND VARIANCES

Our model for group size (NUMIND) included the following explanatory variables: 1) lion densities (LION: obtained from Lee et al. 2016a, b; as lions/100 km^2); 2) distance (km) from nearest boma (D_BOMA) and nearest town (D_TOWN); 3) general vegetation type from densest to most open (deciduous bushland and thicket [BD], wooded grassland [WD], grassland on volcanic soils with scattered woody species [GV]; grassland on flooded soils [G]); 4) specific primary forage type (*D. cinerea* [DICHRO], *A. tortilis* [ATORT], *A. drepanolobium* [ADREP], *Combretum* [COMB], and non-specific [NONSP]); 5) season (Jan–Feb [SHORTR], May–June [LONGR], Sep–Oct [DRY]); 6) time of day, including the quadratic form (HOUR and $HOUR^2$); and 7) social covariates: local giraffe population density (POPDEN) as giraffes/km^2, proportion of adults that were male (P_AM), and proportion of the group that were calves (P_C). We also modelled interactions between proportion of calves and general vegetation and specific primary forage type; general vegetation and specific primary forage type and lion density; specific primary forage type and season; we further modelled three-way interactions among proportion of calves, season, and general vegetation; and proportion of calves, lion density, and general vegetation. We included an effect of time of day because natural predators are most active at

night (Mogensen et al. 2011), and we predicted larger groups early in the morning and late in the afternoon, particularly in high-cover vegetation where lions tend to hunt (Hopcraft et al. 2005). Proportional explanatory variables were arcsine-transformed to meet assumptions of normality. We specified priors on likelihoods for the variance components, with variance and degree of belief parameters for random effects and residuals set to 1, prior means set to 0, and prior covariance matrix set to 1000 (sensu Hadfield 2010).

In our first group composition analysis, we regressed the proportion of calves in a group on lion density, season, distance to bomas and towns, and general vegetation and specific primary forage types, as well as the interaction between season and general vegetation; lion density and general vegetation, and lion density and season (to account for variation in lion predation pressure on giraffe calves by season: Lee et al. 2016b). We used a "multinomial2" distribution with the binomial specification. Prior specification of variance was set to 1 and the degree of belief parameter set to 0.002, which is a frequently used prior specification for variance components (Hadfield 2010).

In our second group composition analysis we conducted multinomial regression where our response variables were the probability of a group being one of five types: a single adult male (SINGLEM), a bachelor herd (BACH), a single adult female (SINGLEF), a mixed-sex/adult female group without calves (MIXED), or a female singleton or group with at least one calf (CALF). Explanatory variables included distance to bomas and towns, general vegetation and specific primary forage types, a season by specific forage type interaction. Models run with lion density failed to converge. We parameterized the multinomial model as a series of binomial contrasts with probability of being a systematic point along our survey transects set as the reference (first factor) category against which the 5 group types were contrasted. We fixed residual variance at 1 for variances and 0 for covariances using the residual constraint

recommended by Hadfield (2010): R=1 and V = 1/*k*(I+J), where *k* is the number of response categories, I is the identity matrix, and J is the unit matrix consisting of all ones.

Categorical explanatory variables of general and specific vegetation types and season were coded as factors with the most common general vegetation type WD, the non-specific primary forage type NONSP, and the season LONGR set as the reference category intercepts, whereas lion density, distance to human habitation, time of day, local giraffe population density, proportion adult males, and proportion of calves were continuous variables.

PARAMETER ESTIMATES FOR ALL PREDICTOR VARIABLES

Table S1. Posterior mean values of fixed effects, 95% credible intervals, and probability of significance for determinants of group size (N=2888 groups) for Masai giraffes (*Giraffa camelopardalis tippelskirchii*) in the Tarangire Ecosystem, northern Tanzania, 2011–2016. Estimates from a generalized linear mixed regression model with a zero-truncated Poisson distribution run for 100,000 iterations with a burn-in phase of 5,000 and thin interval of 100. Group identification was considered a random effect to account for non-independence of group members. Predictor values whose credible intervals do not overlap zero are bolded.

Variable[a]	Posterior Mean of ß Estimate[b]	Lower 95% CI	Upper 95% CI	pMCMC
(Intercept)	-0.485	-1.234	0.249	0.171
POPDEN	0.174	-0.198	0.566	0.389
LION	0.009	-0.044	0.062	0.747
shortr	0.034	-0.204	0.313	0.798
dry	**-0.362**	**-0.650**	**-0.102**	**0.021**
hour	**0.300**	**0.189**	**0.416**	**< 0.001**
hour2	**-0.011**	**-0.016**	**-0.007**	**< 0.001**
asin(P_AM)	**-0.623**	**-0.703**	**-0.534**	**< 0.001**
asin(P_C)	1.203	-0.058	2.788	0.118
D_Boma	0.000	-0.013	0.010	0.928
D_Town	0.003	0.000	0.007	0.082
GENVEGbd	0.492	-0.128	1.143	0.147
GENVEGg	0.647	-0.384	1.754	0.244
GENVEGgv	0.215	-0.319	0.652	0.398
SPVEGadrep	-0.207	-0.878	0.415	0.541
SPVEGatort	-0.170	-0.437	0.114	0.211
SPVEGcomb	-1.015	-1.906	0.035	0.057
SPVEGdichro	-0.036	-0.466	0.332	0.886
dry:SPVEGadrep	0.080	-0.393	0.473	0.695
dry:SPVEGatort	0.002	-0.227	0.208	0.977

dry:SPVEGcomb	**1.144**	**0.291**	**2.013**	**0.006**
dry:SPVEGdichro	-0.287	-0.583	0.026	0.065
shortr:SPVEGadrep	0.257	-0.190	0.661	0.246
shortr:SPVEGatort	0.057	-0.173	0.271	0.623
shortr:SPVEGcomb	**0.793**	**-0.014**	**1.553**	**0.040**
shortr:SPVEGdichro	0.038	-0.291	0.338	0.827
hour:GENVEGbd	-0.032	-0.073	0.002	0.091
hour:GENVEGg	-0.044	-0.122	0.044	0.297
hour:GENVEGgv	-0.012	-0.042	0.015	0.404
LION:dry	0.001	-0.022	0.024	0.907
LION:shortr	0.009	-0.011	0.031	0.404
LION:SPVEGadrep	-0.001	-0.048	0.044	0.998
LION:SPVEGatort	0.008	-0.014	0.032	0.549
LION:SPVEGcomb	0.007	-0.090	0.099	0.865
LION:SPVEGdichro	0.008	-0.026	0.039	0.646
LION:GENVEGbd	-0.010	-0.061	0.035	0.667
LION:GENVEGg	-0.019	-0.094	0.071	0.648
LION:GENVEGgv	-0.007	-0.043	0.029	0.688
asin(P_C):SPVEGadrep	0.060	-0.764	0.953	0.931
asin(P_C):SPVEGatort	-0.010	-0.428	0.420	0.977
asin(P_C):SPVEGcomb	-0.411	-2.210	1.694	0.705
asin(P_C):SPVEGdichro	-0.108	-0.898	0.609	0.802
asin(P_C):GENVEGbd	0.391	-1.710	2.432	0.701
asin(P_C):GENVEGg	-0.157	-3.414	2.839	0.903
asin(P_C):GENVEGgv	-0.340	-2.093	1.309	0.697
dry:asin(P_C):GENVEGwd	0.215	-0.454	0.980	0.545
dry:asin(P_C):GENVEGbd	0.299	-0.769	1.250	0.594
dry:asin(P_C):GENVEGg	-0.284	-3.251	2.586	0.846
dry:asin(P_C):GENVEGgv	0.121	-0.616	0.773	0.714
shortr:asin(P_C):GENVEGwd	-0.266	-0.883	0.414	0.448
shortr:asin(P_C):GENVEGbd	0.204	-0.982	1.338	0.676
shortr:asin(P_C):GENVEGg	0.145	-2.273	2.529	0.903
shortr:asin(P_C):GENVEGgv	-0.599	-1.362	0.041	0.086
LION:asin(P_C):GENVEGwd	-0.115	-0.250	0.041	0.154
LION:asin(P_C):GENVEGbd	**-0.105**	**-0.179**	**-0.019**	**0.017**
LION:asin(P_C):GENVEGg	0.076	-0.321	0.486	0.701
LION:asin(P_C):GENVEGgv	-0.041	-0.129	0.037	0.352

[a] POPDEN=local giraffe population density in 5 administrative sites: Tarangire and Lake Manyara National Parks, Manyara Ranch Conservancy, Mtowambu and Lolkisale Game Controlled Areas (#giraffes/km^2); LION=local lion density in 5 administrative sites (#lions/100 km^2); Season: dry (Sep-Oct), shortr (short rains, Jan-Feb) as compared with reference category long rains (May-Jun); Time of day (hour); P_AM=adult males/adult males+adult females; P_C=number of calves/number of individuals in group (both proportions arcsin-transformed); D_Boma=distance to nearest boma (Masai family compound) in km; D_Town=distance to permanent town in km; General vegetation type (GENVEG): bd (deciduous bushland and thicket), g (grassland on flooded soils), gv (grassland on volcanic soils) as compared with reference category wd (wooded grassland); Specific primary forage type (SPVEG): dichro (*Dichrostachys cinerea*), comb (*Combretum spp.*), adrep (*Acacia drepanolobium*), and atort (*Acacia tortilis*) compared with reference category nonspecific (NONSP).

[b] NumInd ~ POPDEN + LION + shortr + dry + hour + hour2 + asin(P_AM) + asin(P_C) + D_Boma + D.Town + GENVEG + SPVEG + SPVEG:dry + SPVEG:shortr + GENVEG:hour + dry:LION + shortr:LION + SPVEG:LION + +GENVEG:LION +

asin(P_C):SPVEG + asin(P_C):GENVEG + GENVEG:asin(P_C):dry + GENVEG:asin(P_C):shortr + GENVEG:asin(P_C):LION

Table S2. Posterior mean values of fixed effects, 95% credible intervals, and probability of significance for determinants of the proportion of calves in a group (N=2888 groups) for Masai giraffes (*Giraffa camelopardalis tippelskirchii*) in the Tarangire Ecosystem, northern Tanzania, 2011–2016. Estimates from a generalized linear mixed regression model with a binomial distribution run for 100,000 iterations with a burn-in phase of 5000 and thin interval of 100. Group identification was considered a random effect. Predictor values whose credible intervals do not overlap zero are bolded.

Variable[a]	Posterior Mean of ß Estimate[b]	Lower 95% CI	Upper 95% CI	pMCMC
(Intercept)	-3.362	-5.280	-1.710	0.008
LION	0.018	-0.152	0.206	0.709
shortr	0.183	-0.411	1.042	0.514
dry	0.153	-0.416	0.870	0.571
D_Boma	**-0.043**	**-0.064**	**-0.023**	**< 0.001**
D.Town	0.007	0.000	0.016	0.069
GENVEGbd	0.580	-0.628	1.707	0.259
GENVEGg	0.457	-1.017	2.151	0.448
GENVEGgv	0.823	-0.528	2.138	0.131
SPVEGadrep	**0.310**	**0.018**	**0.570**	**0.040**
SPVEGatort	0.180	0.010	0.343	0.051
SPVEGcomb	-0.494	-1.064	0.073	0.093
SPVEGdichro	-0.071	-0.276	0.126	0.507
dry:GENVEGbd	-0.281	-0.814	0.324	0.305
dry:GENVEGg	-0.408	-1.248	0.462	0.347
dry:GENVEGgv	-0.005	-0.344	0.368	0.958
shortr:GENVEGbd	0.307	-0.253	0.905	0.312
shortr:GENVEGg	-0.156	-1.042	0.812	0.714
shortr:GENVEGgv	-0.017	-0.401	0.360	0.905
LION:GENVEGbd	-0.022	-0.167	0.112	0.625
LION:GENVEGg	-0.014	-0.189	0.157	0.819
LION:GENVEGgv	-0.064	-0.219	0.076	0.225
LION:dry	0.005	-0.068	0.065	0.863
LION:shortr	-0.011	-0.076	0.067	0.697

[a] LION=local lion density in 5 administrative sites: Tarangire and Lake Manyara National Parks, Manyara Ranch Conservancy, Mtowambu and Lolkisale Game Controlled Areas (#lions/100 km^2); Season: dry (Sep-Oct), shortr (short rains, Jan-Feb) as compared with reference category long rains (May-Jun); Time of day (hour); D_Boma=distance to nearest boma (Masai family compound) in km; D_Town=distance to permanent town in km; General vegetation type (GENVEG): bd (deciduous bushland and thicket), g (grassland on flooded soils), gv (grassland on volcanic soils) as compared with reference category wd (wooded grassland); Specific primary forage type (SPVEG): dichro (*Dichrostachys cinerea*), comb (*Combretum spp.*), adrep (*Acacia drepanolobium*), and atort (*Acacia tortilis*) compared with reference category nonspecific.

[b] cbind(Calf, NumInd) ~ LION + shortr + dry + D_Boma + D.Town + GENVEG + SPVEG + dry:GENVEG + shortr:GENVEG + GENVEG:LION + dry:LION + shortr:LION

Table S3. Posterior mean values of fixed effects, 95% credible intervals, and probability of significance for determinants of probability of a bachelor herd, single male, single female, or calf group compared to reference factor mixed-sex group with no calves (N=2888 groups) for Masai giraffes (*Giraffa camelopardalis tippelskirchii*) in the Tarangire Ecosystem, northern Tanzania, 2011–2016. Estimates from a generalized linear mixed multinomial regression model with a categorical distribution run for 100,000 iterations with a burn-in phase of 5000 and thin interval of 100. Group identification was considered a random effect. Predictor values whose credible intervals do not overlap zero are bolded.

Variable[a]	Posterior Mean of ß Estimate[b]	Lower 95% CI	Upper 95% CI	pMCMC
traitTYPE.BACH:D_Boma	**0.230**	**0.120**	**0.360**	**< 0.001**
traitTYPE.CALF:D_Boma	**-0.190**	**-0.310**	**-0.080**	**< 0.001**
traitTYPE.MIXED:D_Boma	0.010	-0.060	0.090	0.785
traitTYPE.SF:D_Boma	-0.010	-0.050	0.020	0.440
traitTYPE.SM:D_Boma	**0.060**	**0.020**	**0.100**	**< 0.001**
traitTYPE.BACH:D.Town	0.000	-0.020	0.030	0.775
traitTYPE.CALF:D.Town	**0.050**	**0.010**	**0.090**	**0.034**
traitTYPE.MIXED:D.Town	0.000	-0.030	0.030	0.987
traitTYPE.SF:D.Town	0.010	-0.010	0.020	0.421
traitTYPE.SM:D.Town	-0.010	-0.020	0.010	0.472
traitTYPE.BACH:SPVEGadrep	2.780	-2.200	8.540	0.535
traitTYPE.CALF:SPVEGadrep	-2.990	-8.740	1.470	0.251
traitTYPE.MIXED:SPVEGadrep	-3.970	-10.440	1.220	0.194
traitTYPE.SF:SPVEGadrep	-1.520	-5.780	3.600	0.398
traitTYPE.SM:SPVEGadrep	2.310	-1.170	6.100	0.491
traitTYPE.BACH:SPVEGatort	0.020	-3.030	3.210	0.987
traitTYPE.CALF:SPVEGatort	1.650	-2.760	5.360	0.448
traitTYPE.MIXED:SPVEGatort	-1.260	-4.290	2.160	0.484
traitTYPE.SF:SPVEGatort	-0.210	-2.230	3.120	0.760
traitTYPE.SM:SPVEGatort	-0.100	-1.360	1.460	0.851
traitTYPE.BACH:SPVEGcomb	3.160	-1.740	9.100	0.276
traitTYPE.CALF:SPVEGcomb	0.050	-9.200	6.380	0.762
traitTYPE.MIXED:SPVEGcomb	-0.090	-5.050	3.940	0.983
traitTYPE.SF:SPVEGcomb	-0.470	-3.310	2.270	0.806
traitTYPE.SM:SPVEGcomb	2.140	-2.850	6.440	0.429
traitTYPE.BACH:SPVEGdichro	-0.070	-2.930	2.820	0.935
traitTYPE.CALF:SPVEGdichro	-6.320	-14.310	2.860	0.259
traitTYPE.MIXED:SPVEGdichro	-1.800	-6.810	2.520	0.486
traitTYPE.SF:SPVEGdichro	**-3.890**	**-7.060**	**-0.200**	**0.027**
traitTYPE.SM:SPVEGdichro	-0.070	-3.700	4.520	0.989
traitTYPE.BACH:GENVEGbd	**-2.720**	**-4.450**	**-1.630**	**< 0.001**
traitTYPE.CALF:GENVEGbd	**2.070**	**0.950**	**3.220**	**< 0.001**
traitTYPE.MIXED:GENVEGbd	-0.740	-1.740	0.320	0.139
traitTYPE.SF:GENVEGbd	**-0.510**	**-1.110**	**-0.050**	**0.046**
traitTYPE.SM:GENVEGbd	**-0.790**	**-1.290**	**-0.250**	**< 0.001**
traitTYPE.BACH:GENVEGg	0.280	-0.910	1.550	0.686

traitTYPE.CALF:GENVEGg	**2.410**	**0.000**	**5.160**	**0.042**
traitTYPE.MIXED:GENVEGg	0.540	-2.310	3.310	0.762
traitTYPE.SF:GENVEGg	-0.370	-1.440	0.770	0.585
traitTYPE.SM:GENVEGg	0.210	-0.870	1.210	0.714
traitTYPE.BACH:GENVEGgv	-0.240	-1.290	0.880	0.701
traitTYPE.CALF:GENVEGgv	**2.560**	**1.160**	**4.200**	**< 0.001**
traitTYPE.MIXED:GENVEGgv	0.900	-0.180	1.910	0.109
traitTYPE.SF:GENVEGgv	0.530	-0.080	1.260	0.131
traitTYPE.SM:GENVEGgv	-0.050	-0.690	0.560	0.947
traitTYPE.CALF:SPVEGadrep:SEASONdry	8.040	-2.140	19.780	0.126
traitTYPE.MIXED:SPVEGadrep:SEASONdry	11.090	-0.780	23.030	0.109
traitTYPE.SF:SPVEGadrep:SEASONdry	5.200	-0.720	10.340	0.133
traitTYPE.SM:SPVEGadrep:SEASONdry	1.230	-5.230	6.280	0.600
traitTYPE.CALF:SPVEGatort:SEASONdry	-0.010	-5.030	3.620	0.901
traitTYPE.MIXED:SPVEGatort:SEASONdry	2.320	-2.180	5.980	0.303
traitTYPE.SF:SPVEGatort:SEASONdry	0.900	-1.690	3.160	0.486
traitTYPE.SM:SPVEGatort:SEASONdry	-0.050	-3.590	3.060	0.905
traitTYPE.CALF:SPVEGcomb:SEASONdry	-3.510	-10.450	5.990	0.419
traitTYPE.MIXED:SPVEGcomb:SEASONdry	2.000	-5.140	9.530	0.579
traitTYPE.SF:SPVEGcomb:SEASONdry	-0.750	-5.030	3.740	0.771
traitTYPE.SM:SPVEGcomb:SEASONdry	-1.520	-4.970	3.240	0.493
traitTYPE.CALF:SPVEGdichro:SEASONdry	7.460	-3.320	18.120	0.299
traitTYPE.MIXED:SPVEGdichro:SEASONdry	5.900	-1.560	13.810	0.152
traitTYPE.SF:SPVEGdichro:SEASONdry	**6.530**	**0.770**	**11.520**	**0.004**
traitTYPE.SM:SPVEGdichro:SEASONdry	1.140	-4.900	7.000	0.884
traitTYPE.CALF:SPVEGadrep:SEASONlongr	7.170	-1.710	17.170	0.149
traitTYPE.MIXED:SPVEGadrep:SEASONlongr	5.330	-5.730	17.420	0.501
traitTYPE.SF:SPVEGadrep:SEASONlongr	4.750	-1.460	11.510	0.219
traitTYPE.SM:SPVEGadrep:SEASONlongr	0.430	-4.820	5.090	0.808
traitTYPE.CALF:SPVEGatort:SEASONlongr	-0.730	-5.680	3.060	0.836
traitTYPE.MIXED:SPVEGatort:SEASONlongr	2.230	-2.220	5.930	0.318
traitTYPE.SF:SPVEGatort:SEASONlongr	0.840	-1.450	2.810	0.522
traitTYPE.SM:SPVEGatort:SEASONlongr	0.790	-2.140	3.060	0.486
traitTYPE.CALF:SPVEGcomb:SEASONlongr	-1.700	-12.550	11.660	0.665
traitTYPE.MIXED:SPVEGcomb:SEASONlongr	4.470	-4.180	13.420	0.343
traitTYPE.SF:SPVEGcomb:SEASONlongr	5.650	-0.760	11.390	0.101
traitTYPE.SM:SPVEGcomb:SEASONlongr	2.480	-2.210	8.080	0.377
traitTYPE.CALF:SPVEGdichro:SEASONlongr	5.150	-4.520	14.760	0.608
traitTYPE.MIXED:SPVEGdichro:SEASONlongr	2.980	-2.620	10.340	0.440
traitTYPE.SF:SPVEGdichro:SEASONlongr	3.890	-0.010	7.990	0.055
traitTYPE.SM:SPVEGdichro:SEASONlongr	-0.120	-4.930	4.980	0.922
traitTYPE.CALF:SPVEGadrep:SEASONshortr	**10.340**	**1.630**	**18.650**	**0.006**
traitTYPE.MIXED:SPVEGadrep:SEASONshortr	7.430	-2.260	18.100	0.185
traitTYPE.SF:SPVEGadrep:SEASONshortr	**5.900**	**0.610**	**11.490**	**0.011**
traitTYPE.SM:SPVEGadrep:SEASONshortr	1.810	-3.070	5.700	0.383

traitTYPE.CALF:SPVEGatort:SEASONshortr	0.790	-4.050	5.140	0.701
traitTYPE.MIXED:SPVEGatort:SEASONshortr	3.680	-0.670	7.160	0.101
traitTYPE.SF:SPVEGatort:SEASONshortr	2.000	-0.640	4.060	0.133
traitTYPE.SM:SPVEGatort:SEASONshortr	1.940	-1.520	4.360	0.236
traitTYPE.CALF:SPVEGcomb:SEASONshortr	4.940	-5.050	16.280	0.402
traitTYPE.MIXED:SPVEGcomb:SEASONshortr	5.620	-1.280	12.130	0.118
traitTYPE.SF:SPVEGcomb:SEASONshortr	**5.950**	**0.890**	**10.850**	**0.029**
traitTYPE.SM:SPVEGcomb:SEASONshortr	2.300	-2.170	8.460	0.440
traitTYPE.CALF:SPVEGdichro:SEASONshortr	7.760	-2.590	18.900	0.272
traitTYPE.MIXED:SPVEGdichro:SEASONshortr	2.960	-3.970	10.620	0.507
traitTYPE.SF:SPVEGdichro:SEASONshortr	4.240	-0.520	8.820	0.086
traitTYPE.SM:SPVEGdichro:SEASONshortr	-0.020	-5.810	5.450	0.994

[a] D_Boma=distance to nearest boma (Masai family compound); D_Town=distance to permanent town; Specific primary forage type (SPVEG): dichro (*Dichrostachys cinerea*), comb (*Combretum*), adrep (*Acacia drepanolobium*), and atort (*Acacia tortilis*) compared with reference category nonspecific; General vegetation type (GENVEG): bd (deciduous bushland and thicket), g (grassland on flooded soils), gv (grassland on volcanic soils) as compared with reference category wd (wooded grassland).
[b] Model = TYPE ~ -1 + trait * D_Boma - D_Boma + trait * D.Town - D.Town + trait * SPVEG - SPVEG + trait * GENVEG - GENVEG + trait * SEASON - SEASON + trait * SEASON:SPVEG

Chapter 2

Proximity to humans affects local social structure in a giraffe metapopulation

Monica L. Bond · Barbara König · Derek E. Lee · Arpat Ozgul · Damien Farine

Submitted to Journal of Animal Ecology

Abstract Experimental laboratory evidence suggests that animals with disrupted social systems express weakened relationship strengths and have more exclusive social associations, and that these changes have functional consequences. A key question is whether anthropogenic pressures have a similar impact on the social structure of wild animal communities. We addressed this question by constructing a social network from 6 years of systematically collected photographic capture-recapture data spanning 1,139 individual adult female Masai giraffes inhabiting a large, unfenced, heterogeneous landscape in northern Tanzania. We then used the social network to identify distinct social communities, and tested whether social or anthropogenic and other environmental factors predicted differences in social structure among these communities. We reveal that giraffes have a multilevel social structure. Local preferences in associations among individuals scale up to distinct, but spatially overlapping, social communities, that can be viewed as a large interconnected metapopulation. We then find that communities that are closer to traditional compounds of indigenous Masai people express weaker relationship strengths and the giraffes in these communities are more exclusive in their associations. The patterns we characterise in response to proximity to humans reflect the predictions of disrupted social systems. Near bomas, fuelwood cutting can reduce food resources, and groups of giraffes are more likely to encounter livestock and humans on foot, thus disrupting the social associations among group members. Our results suggest that human presence could potentially be playing an important role in determining the conservation future of this megaherbivore.

Keywords giraffe, *Giraffa camelopardalis*, social network analysis, community detection, anthropogenic disruption

Introduction

Sociality provides the channel through which information, genetic material, and diseases spread through populations (Kurvers, Krause, Croft, Wilson, & Wolf, 2014; Sih, Spiegel, Godfrey, Leu, & Bull, 2018). Social interactions among group members can be critical for survival and reproduction in group-living species (Alberts, 2019; Alexander, 1974) and are essential for the persistence of social units (Dunbar & Shultz, 2010). Social behaviour of animals can respond to changes in the environment (Edenbrow et al., 2011) or habitat configuration (He, Maldonado-Chaparro, & Farine, 2019; Lattanzio & Miles, 2014; Leu, Farine, Wey, Sih, & Bull, 2016). Increasingly, this environment includes disturbances arising from proximity to humans (Belton, Cameron, & Dalerum, 2018). Repeated, minor, and indirect disruptions, such as human presence and encroachment into natural habitats, might accumulate to have cryptic negative effects on social behaviour. These effects might be especially prominent in animals with larger space requirements and a history of hunting or harassment by humans, and therefore lower tolerance to human presence.

There is increasing evidence that human activities can have far-reaching consequences to social species by disrupting group structure, and subsequently impacting group function (Foley & Faust, 2010; Parsons, Balcomb, Ford, & Durban, 2009; Shannon et al., 2013). African elephants exposed to traumatic events such as selective killing of older family members were unable to discriminate between calls of conspecifics (Shannon et al., 2013) and displayed less discriminating social behaviour (Gobush & Wasser, 2009). However, human impacts could also be more subtle. Socially stable colonies of zebra finches (*Taeniopygia guttata*) that were

experimentally split and then recombined expressed weaker relationship strengths and were more exclusive in their social associations, despite experiencing no long-term change in group membership. This change in social structure then resulted in lower group foraging efficiency (Maldonado-Chaparro, Alarcon-Nieto, Klarevas-Irby, & Farine, 2018). In another study, tree lizards (*Urosaurus ornatus*) living in frequently burned compared with unburned habitats were more aggressive and interacted more often with each other (Lattanzio & Miles, 2014). Spotted hyena (*Crocuta crocuta*) clans that experienced the highest human activity interacted less with other clan members (Belton, Cameron, & Dalerum, 2018). Together, these studies suggest a link between externally mediated social disruptions and social function.

Detecting signals of natural versus anthropogenic influences on social relationships among individuals in their natural environment is challenging. It requires large-scale studies of individually identified animals across replicated social groups spanning multiple environmental gradients. Here, we addressed this challenge by collecting and analysing long-term data from a metapopulation of adult female Masai giraffes (*Giraffa camelopardalis tippelkirchii*) in Tanzania, and testing whether the environment—especially proximity to human settlements—shapes social structure. Giraffes are megaherbivores that can roam over vast areas, moving across ecologically heterogeneous landscapes that, increasingly, include anthropogenically modified land and human settlements (Knüsel, Lee, König, & Bond, 2019; Lee & Bolger, 2017). Adult females maintain family-based long-term associations (Bercovitch & Berry, 2012; Carter, Seddon, Frère, Carter, & Goldizen, 2013) despite having fluid group membership via fission-fusion dynamics (Leuthold, 1979). Such associations have been proposed to result in a multi-level social structure (VanderWaal, Wang, McCowan, Fushing, & Isbell, 2014), although the spatial reach of, and overlap among, giraffe social communities remains unknown.

In Tanzania, giraffes are generally tolerated by humans because they do not cause conflicts with farmers or livestock. Hunting of giraffes is illegal, but poaching for meat and body parts occurs (Kiffner, Peters, Stroming, & Kioko, 2015). Despite the public tolerance and hunting restrictions, Masai giraffe populations throughout their range have declined 50% in recent years (Bolger et al., 2019). Several reasons have been suggested, including poaching, habitat loss and fragmentation, lion (*Panthera leo*) predation on calves, and changes in food supply (Lee, 2018; Muller, 2018; Strauss, Kilewo, Rentsch, & Packer, 2015). Disruption to social systems also may be a contributing factor in population declines, but, to date, anthropogenic effects on social structure of giraffes remain unclear. One recent study by Muller *et al*. (2019) reported differences in network metrics across two separated, small, enclosed populations of Rothschild's giraffes in Kenya. They found that relationships were weaker and more exclusive in a population inhabiting an area with a high volume of tourists and lions, compared to another population inhabiting an area with no lions and a low volume of tourists. Unfortunately, Muller *et al*. (2019) did not statistically compare the network characteristics of the two populations, and the effects of natural predation and human disturbance from tourism could not be discriminated due to the lack of replication beyond the two populations. In our study area, overlapping (i.e. replicated) communities of giraffes occurred along a gradient of proximities to human settlements, enabling us to test the effects on social structure from human presence. Giraffes do not flee from and appear to be tolerant of tourist vehicles in protected areas, so we did not consider tourism traffic in the protected areas to disrupt social structure.

In this paper, we examine whether proximity to human settlements can affect the social relationships of adult female giraffes. We focused on adult females because they form longer-term associations with other females than do adult males, show stronger preferences in their associations (Berkovitch & Berry, 2012; Carter, Brand, Carter, Shorrocks, & Goldizen, 2013).

Further, adult females have more stable association rates than maturing and dispersing subadult females (Carter, Brand, Carter, Shorrocks, & Goldizen, 2013). Giraffes in Tanzania are poached using machetes (Kiffner, Peters, Stroming, & Kioko, 2015) or snares (Strauss, Kilewo, Rentsch, & Packer, 2015) and are intolerant of people approaching them on foot. Further, livestock herders are often accompanied by dogs, which chase giraffes (MLB and DEL, personal observation). Thus we expect being near to human settlements and the consequent presence of humans on foot could disrupt the natural social behaviours of giraffes by scattering—thus splitting—members of a group. People often cut wood for fuel, which may reduce food resources for giraffes near bomas and further contribute to disruption of their social behaviours during foraging. Based on the results of Maldonado-Chaparro *et al.* (2018), we predict that if giraffes cannot maintain as large group sizes because groups living near humans are repeatedly disturbed, they should preferentially associate with fewer individuals, thus reducing the average relationship strength and being more exclusive in their social associations, likely because instability increases the costs of maintaining many concurrent relationships. To test this prediction, we constructed social networks using individual-based photographic capture-recapture data systematically collected over 6 years from a metapopulation of 1,139 wild adult female giraffes in a large and ecologically diverse area of northern Tanzania: the Tarangire Ecosystem. Our study area spans two national parks, a private ranch, and unprotected village lands (Fig. 1). Because these areas are unfenced, individuals can move across the entire area. While the parks are protected, village lands are not, and these are experiencing rapid land-use changes such as conversion of natural savanna habitats to farmland (Lee, Bond, Kissui, Kiwango, & Bolger, 2016; Msoffe et al., 2011).

Animals often associate in groups that merge and split over time in a fission-fusion process, but may form social communities of individuals that interact frequently with each other

in an area (Shizuka & Farine, 2016). Our first objective was to determine whether adult female giraffes form discrete communities of individuals that associate more frequently within the larger metapopulation, and if so, how many communities are there and how modular are they? Partitioning the giraffe metapopulation that spans the Tarangire Ecosystem into multiple distinct communities then allowed us to accomplish our second objective, to identify natural and anthropogenic factors that explain variation in sociality. We modelled the community-level relationship strength and social exclusivity as functions of social and environmental factors, including local giraffe population density, vegetation fertility, and distance to two different types of human settlements, bomas and towns. Bomas are dispersed family compounds of huts constructed with natural materials, and towns consist of dense concentrations of concrete structures. Bomas in our study area are occupied by indigenous pastoralist Masai people who typically do not poach giraffes for meat, but may kill lions and other carnivores to protect livestock (Kissui, 2008) and lion and spotted hyena densities are significantly lower in adjacent village lands than in the parks (Lichtenfeld, 2005). Towns are much rarer, but also much more densely populated by people, typically surrounded by farmlands, and inhabited by bushmeat poachers (Kiffner, Peters, Stroming, & Kioko, 2015). We hypothesized that social communities of giraffes living closer to both types of human settlements would exhibit weaker relationship strengths and more exclusive social associations—a signature of a disrupted social environment according to Maldonado-Chaparro *et al.* (2018).

Methods

STUDY AREA

The Tarangire Ecosystem (TE) in northern Tanzania is in the eastern branch of the Great Rift Valley and encompasses roughly 30,000 km^2 (Prins, 1987). The TE experiences three

precipitation seasons per year (short rains = Oct–Jan, long rains = Feb–May, and dry = Jun–Sep). The main vegetation communities in the TE are *Acacia tortilis* parkland, *Acacia-Commiphora* woodland, gall *Acacia drepanolobium* woodland, *Combretum-Dalbergia* woodland, and open grassland (Lamprey, 1963). The TE has undergone 3% annual human population growth between 2003 and 2012, which added nearly 800,000 people (TNBS, 2013), increased illegal poaching, caused habitat loss and fragmentation, and reduced connectivity for wildlife (Msoffe et al., 2011).

Our study area is at the core of the TE, where we sampled a 1,500 km^2 area spanning five administrative units with differing management activities (Fig. 1). The two national parks, Tarangire (TNP) and Lake Manyara (LMNP), have high levels of wildlife protection including exclusion of livestock and human settlements and regular anti-poaching patrols; Manyara Ranch Conservancy (MRC) has intermediate levels of wildlife protection with exclusion of human settlements and some anti-poaching patrols, but with large numbers of livestock and herders present during the daytime. Lolkisale (LGCA) and Mtowambu Game Controlled Areas (MGCA) have the lowest levels of wildlife protection and allow sport hunting, livestock, and human settlements. None of the administrative units are fenced, and all units are connected by movements of adult female giraffes (Lee & Bolger, 2017).

The Rift Valley escarpment, forming the western boundary of the study area, is a steep cliff that restricts giraffe movements in that direction. Few wild large mammals are present east of Makuyuni town, west of TNP, and south of LMNP due to high human and livestock population density and intensive agriculture. Two 2-lane asphalt roads cross the study area, but giraffes can cross these (Lee & Bolger, 2017).

FIELD DATA COLLECTION

Each giraffe has a coat pattern that is unique and unchanging from birth to death (Foster, 1966). We used a Canon EOS 7D Mark II with a 100-400 mm lens to photograph, and later identify, individual giraffes from their unique coat markings. From May 2011 until October 2016, we conducted 31 daytime, fixed-route transect surveys along a network of dirt tracks to collect photographic capture-mark-recapture data on three primary sampling periods per year near the end of each precipitation season (Jan–Feb, May–Jun, and Sep–Oct). We sampled according to Pollock's robust design with each primary sampling period composed of two independent, back-to-back secondary sampling periods during which all transects in the study area were driven once (Pollock, 1982). Transect density throughout the study area was high (0.42 km/km^2) relative to average adult female giraffe home range (115 km^2; Knüsel, Lee, König, & Bond, 2019). Driving speed was maintained between 15 and 20 km on all transects, and all surveys included the same two observers and driver. Each secondary survey took approximately 10 days.

When giraffes were encountered, we 'captured' (or 'recaptured') each animal by approaching to within 150 m distance and photographing them on the right side for individual identification. We attempted to find and photograph all members of all groups we encountered, however, some individuals inevitably escaped detection or identification (see *SI Appendix 1*). For each photograph, we recorded the animal's age class (calf, subadult, adult), sex (male, female), and the GPS location of the group. We used physical characteristics, including body shape, relative length of the neck and legs, ossicone characteristics, and height to categorise giraffe into three age classes: calf (< 1 year), subadult (1–3 years), or adult (> 3 years). Giraffes mature sexually at about 4 years of age, so we considered individuals > 3 years to be adults (Lee & Strauss, 2016). In our analysis, we used only females that were adults during the first year of our study. Our sample included most of the adult females in the study area, as 80% were identified

by the end of 2012 (*SI Fig. S1*). To identify individuals, we used Wild-ID, a computer program that matches unique patterns from photographs and is known to perform with little misidentification error in large giraffe datasets (Bolger, Morrison, Vance, Lee, & Harid, 2012). We defined a group as one or more giraffes that were foraging or moving together, but were not moving past each other in opposite directions, and were $\geq$ 500 m from the next nearest giraffe. Giraffe groups were usually self-defining as the distances between individuals were substantially less within groups than between groups.

SOCIAL NETWORK CONSTRUCTION

We used the 'gambit of the group', the presence of two individuals in the same group, to define associations between adult female giraffes and construct a social network (Franks, Ruxton, & James, 2010). We defined the association rate among individuals (the edge weights) using the simple ratio index (Hoppitt & Farine, 2018), which represents the propensity for two individuals to be observed in the same group given that the group contains at least one of the individuals (Farine & Whitehead, 2015). Higher edge weights represented a greater propensity for two individuals to be seen in the same groups. Because individual-level network metrics can vary with sampling effort, population size, and population density, we sought to reduce sampling error by collecting individual data with equal sampling intensity and effort (Farine & Whitehead, 2015). We used only one detection per individual giraffe for each secondary sampling period (~ 10 days) to avoid non-independence of observations and to reduce sampling bias. We further removed individuals with fewer than 6 observations to improve the accuracy of our network (Davis, Crofoot, & Farine, 2018).

We created the social network using the package *asnipe* (Farine, 2013) for R version 3.4.3 (R Core Team, 2017). We show that our results are consistent when using the alternative and

commonly used half-weight index, and when using alternative thresholds ($\geq$ 8 and $\geq$ 10 detections) for the number of observations (Farine & Whitehead, 2015; *SI Appendix 1*). We also used methods recommended by Whitehead (2008a) to explore the robustness of our network (*SI Appendix 2*).

CHARACTERISING COMMUNITY STRUCTURE

Our first objective was to identify and characterise social communities of interacting giraffes in the metapopulation. We used the cluster-walktrap community-detection algorithm to divide the metapopulation into communities using package *igraph* for R (Csárdi & Nepusz, 2006). The strength of the partitioning of the network into discrete communities can be described using a modularity coefficient known as *Q* (Newman, 2003), where higher *Q* values reflect more dense connections within than between communities (Newman, 2006; Shizuka & Farine, 2016). Here we present results from the cluster-walktrap algorithm, but we also ran three other community-detection algorithms and compared *Q* values for each of the three datasets (see *SI Appendix 3*, *Table S1*). We tested whether the metapopulation was more structured into communities than expected by chance given our observation data by noting whether the value of *Q* from the observed network fell outside the 95% range of *Q* values calculated from 1,000 randomly generated networks from permuted data (Shizuka & Farine, 2016). The *P*-value was equivalent to the number of times the observed *Q* ($Q_{observed}$) was higher than the distribution of *Q* values from the randomised networks (Q_{random}). We provide more details on the randomisation procedure below.

We also tested robustness of our community detection using the approach described by Shizuka and Farine (2016). This procedure estimates the effect of sampling effort as the probability that a pair of giraffes that were assigned to the same community in the observed

network was assigned to the same community in 1,000 bootstrapped replicate networks. The test statistic, r_{com}, approaches 1 when all bootstrap replicates result in the exact same community assignments as the observed community, with more robust data having higher r_{com} values. We calculated r_{com} with package *assortnet* for R (Farine, 2016).

IDENTIFYING PREDICTORS OF BETWEEN-COMMUNITY DIFFERENCES IN SOCIAL STRUCTURE

Our second objective was to explore social and environmental factors that might underpin differences in relationship strength and social exclusivity among the discrete communities of giraffes. That is, we split the metapopulation network into replicated but distinct social networks that represent each community, thus making community networks the units of analysis in our study. We then calculated the relationship strength (mean of the edge weights) and the coefficient of variation (CV) of edge weights for all edges pooled in each of these networks. The relationship strength is a measure of the general gregariousness of the members of a community, with higher values suggesting that individuals are, on average associating with a larger number of conspecifics (Whitehead, 2008b). The CV is an index of social differentiation that characterises the propensity for sets of individuals to form preferred relationships within a community (Farine & Whitehead, 2015), and represents the relative investment by individuals into many occasional associates versus fewer, but more frequent, associates. We interpret an increase in the CV as strengthening some relationships and weakening others, thus resulting in more exclusive relationships.

We used linear models (family=Gaussian) to estimate effects of social and environmental predictor variables on first, relationship strength and second, social exclusivity, calculated for each community network. Predictors included (1) the local giraffe population density within the

community (PopDen), equivalent to the number of all adult females ever seen within the boundaries of a community's home range (regardless of community membership or number of detections; N_{total} =1,139), divided by that community's home range size (km^2); (2) the average distance (in km) between all locations of all individuals in a community to the nearest boma (Dist_boma) or town (Dist_town); and (3) the proportion of grasslands on volcanic soils (Prop_gv) within each community's home range. Volcanic soils are particularly fertile, which may enhance forage quality (Mizota, Domon, & Yoshida, 1992), and in our study area volcanic soil grasslands had the highest giraffe calf survival (Lee, Bond, Kissui, Kiwango, & Bolger, 2016). We postulate that adult female giraffes might congregate in areas with high forage nutritional quality and form stronger relationships with others utilizing these resources. These explanatory variables represented potential social, anthropogenic, and vegetation influences on social structure (Table 1, SI Table S2). See SI Appendix 3 for methods used to generate spatial data.

We estimated the significance of each predictor by comparing the coefficient value of the model fitted to the observed community network to the distribution of coefficient values generated by fitting the model to randomised networks generated by the pre-network permutation test as described below.

Comparing network metrics among our giraffe communities was appropriate because all data were collected identically, ensuring observed differences were likely to be biological rather than methodological (Farine, 2017; Farine & Whitehead, 2015). However, it was recently suggested that using pre-network permutation is essential to avoid spurious inference (Farine & Aplin, 2019). That is, rather than directly comparing network metrics to each other (e.g. by directly interpreting the coefficient values of the linear model), which is not possible (Anderson, Butts, & Carley, 1999), we compared the observed differences among communities to the

distribution of differences drawn from all of the random networks generated using the same observation data.

PERMUTATION TESTS FOR HYPOTHESIS TESTING

The non-independent nature of social network data violates assumptions of many statistical methods (Croft, Madden, Franks, & James, 2011; Farine, 2017). Null models can be used to generate patterns expected from the data in the absence of the process of interest (Farine, 2017). We used a modification (Whitehead, 1999) of the Monte Carlo permutation test (Bejder, Fletcher, & Bräger, 1998) to generate randomised networks for hypothesis testing. The algorithm involves sequentially swapping observations of two individuals seen in different groups. In doing so, it inherently controls for many aspects of how the data were collected by generating random networks based on the same number of individuals, where each individual has the same number of observations, controlling for individuals' distributions in space and time, and maintaining the same distribution of group sizes (Farine, 2017). From these networks, we created a distribution of coefficient values from which we obtained a *P*-value that represented the proportion of times the coefficient values from the permuted networks were more extreme than those of the observed networks (Farine, 2017). We performed pre-network permutations using package *asnipe* for R (Farine, 2013).

To control for time, we restricted all swaps to occur within the same 20-day primary sampling period (n = 16 periods). To control for space, we constrained swaps to occur only between groups observed in the same administrative unit (TNP, MRC, LMNP, LGCA, MGCA). After each swap, we re-calculated the edge weights in the network and re-ran exactly the same statistical procedure as we applied to the observed data. For tests determining the community social structure within the metapopulation and assessing robustness of community assignments,

we conducted the permutation procedure on the whole network with 1,000 randomisations. When testing models about predictors of social structure within communities, we conducted the permutation procedure in each community independently (i.e. never swapping individuals across communities because we were interested in understanding within-community processes) and fit the model to 50,000 (relationship strength) or 10,000 (social exclusivity) randomised networks. The difference in the number of permutations reflects differences in how long the *P*-values took to stabilise (see Bejder, Fletcher, & Bräger, 1998).

For descriptive statistics, we calculated the 95% confidence intervals using 100 bootstrapped replicates of our observation data.

Results

COMMUNITY DETECTION

Our social network comprised 540 adult females (with $\geq$ 6 detections over 6 years from a total of 1,944 unique group observations; see Methods, *SI Appendix 1*, *Table S1*). Applying a cluster-walktrap algorithm (see *SI Table S1* for a quantitative comparison of different algorithms) revealed 14 distinct communities of socially associated giraffes in this social network. Using a permutation test, we confirmed that communities in this giraffe population are more structured than expected by chance ($Q_{observed}$ = 0.742, Q_{random} = 0.661, $P < 0.001$), and a bootstrap test revealed that our community assignment was robust (r_{com} = 0.749). Both the $Q_{observed}$ and r_{com} values for our community assignments were relatively high (Shizuka & Farine, 2016), indicating strong community structure and high community fidelity with a low propensity for individuals to mix with other communities. Three of the communities contained $\leq$ 6 individual giraffes. We omitted these three communities from further analysis due to small sample sizes. The remaining 11 communities contained a mean of 47.8 individuals (SD = 16.2, range = 14–70; *SI Table S2*).

These communities overlapped considerably in space (Fig. 1). All communities produced calves, so we did not consider presence versus absence of calves as an influence on social structure.

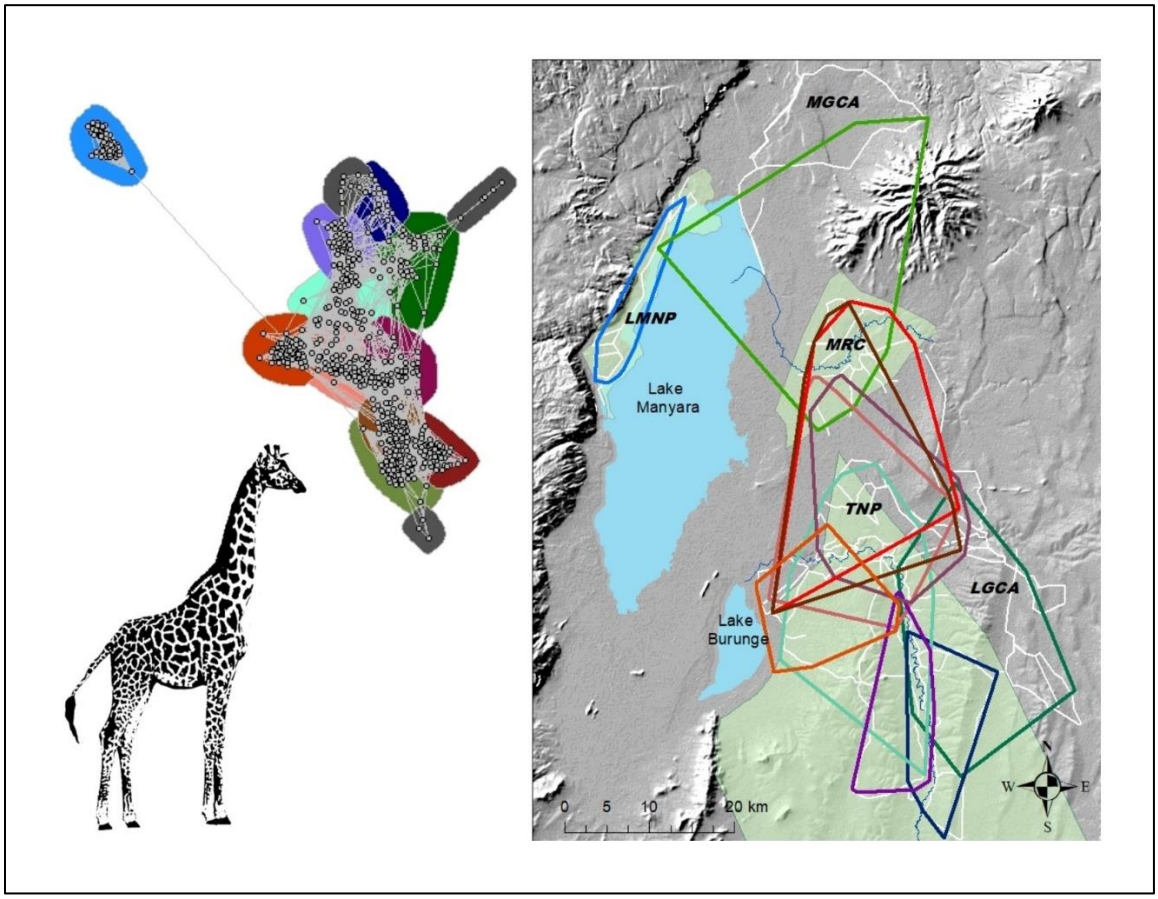

Figure 1. Community structure of a social network of 540 wild adult female giraffes (left) and minimum convex polygons showing spatial overlap of 11 communities (right) in the Tarangire study area, northern Tanzania. Communities were identified with the cluster-walktrap community-detection algorithm. White lines are roads and tracks surveyed for giraffes from 2011–2016, blue lines are rivers, light blue areas are alkaline lakes, and green areas are national parks and conservancies. LMNP = Lake Manyara National Park, TNP = Tarangire National Park, MRC = Manyara Ranch Conservancy, MGCA = Mtowambu Game Controlled Area, and LGCA = Lolkisale Game Controlled Area. Communities 1=dark green, 2=bright blue, 3=navy blue, 5=aquamarine, 6=olive green, 7=salmon, 8=purple, 9=dark pink, 10=red, 13=brown, 14=orange. In the network, communities 4, 11, and 12 are dark grey and contained too few individuals for analysis.

Fission-fusion dynamics, where adult female giraffes form subgroups containing a few other members from their community and where membership fluctuates over time, resulted in relatively weak relationship strengths. The mean relationship strength (edge weight, calculated using the simple ratio index) among giraffes across the whole metapopulation was 0.004 (SD = 0.022, 95% CI = 0.00016–0.006). Even among associated individuals, relationship strength was

relatively low (mean non-zero edge weight = 0.058, SD = 0.234, 95% CI = 0.006–0.110). However, differences in relationship strength among communities varied extensively (range = 0.019–0.078; *SI Table S2*). Within each of the 11 of the giraffe communities we studied, the observed mean edge weight and observed CV values were significantly higher than expected by chance (*SI Table S2*). Together, these results signify that adult female giraffes exhibit preferred and avoided relationships within communities that overlap in space and time with other communities.

PREDICTORS OF WITHIN-COMMUNITY SOCIAL STRUCTURE

Communities of adult female giraffes closer to bomas have weaker average edge weights, suggesting that they have weaker relationship strengths among all the members of the community (Table 1). The edge weight CV of communities also increased significantly with proximity to bomas, indicating that giraffes in communities closer to traditional human compounds exhibit stronger relationships but with fewer other females, indicating greater exclusivity in their social associations (Table 1). Local giraffe population density, distance to towns, and proportion of grasslands on volcanic soils had no discernible influence on variation in community-level social structure (Table 1).

Table 1. Effects of covariates on relationship strength (mean edge weight)[1] and social exclusivity (edge weight CV)[2] of 11 adult female Masai giraffe communities in Tanzania, 2011–2016. *P*-value is the number of times the coefficient generated from 50,000 randomised networks (relationship strength) and 10,000 randomised networks (social exclusivity) was greater than the coefficient from the observed network. Significant *P*-values are given in bold.

	Giraffe population density			
	Estimate	SE	t-value	P_{rand}
Relationship strength	0.002	0.007	0.218	0.810
Social exclusivity	-0.105	0.093	-1.128	0.998
	Distance to boma			
	Estimate	SE	t-value	P_{rand}
Relationship strength	**0.003**	**0.002**	**1.757**	**0.000**
Social exclusivity	**-0.057**	**0.026**	**-2.172**	**0.016**
	Distance to town			
	Estimate	SE	t-value	P_{rand}
Relationship strength	0.000	0.001	0.383	0.258
Social exclusivity	0.002	0.013	0.119	0.987
	Proportion grasslands on volcanic soils			
	Estimate	SE	t-value	P_{rand}
Relationship strength	0.020	0.021	0.957	0.084
Social exclusivity	-0.439	0.282	-1.554	0.919

[1] model = glm(mean edge weight ~ PopDen + Dist_boma + Dist_town + Prop_gv, family=gaussian)
[2] model = glm(edge weight CV ~ PopDen + Dist_boma + Dist_town + Prop_gv, family=gaussian)

Discussion

Our observations of groups of adult female Masai giraffes in the Tarangire Ecosystem revealed that they form somewhat discrete, relatively large social communities that overlap substantially in space, resulting in an interconnected metapopulation. We find that the relationships among individuals within those communities are affected by the presence of traditional human settlements. Communities of giraffes that live closer to bomas have weaker relationship strengths among all community members, and have more exclusive social

associations with fewer other females, in line with our predictions. Proximity to humans therefore appears to play a potentially important role in mediating patterns of social associations between female giraffes in northern Tanzania.

The large spatial scale, absence of fences, and variation in predominance of human influences in our study area, and sizable number of individuals in our study population were key to establishing that human presence can impact strength of relationships and social exclusivity. Relationships were weaker among all community members, and social exclusivity was higher in communities closer to bomas. But what could cause these patterns? The disruption in the equality of relationships could be a result of human habitat modification such as fuelwood cutting near bomas, competition with livestock, or wariness of humans, driving female giraffes to move more often and, when doing so, fission into smaller groups. The greater difficulty in maintaining group cohesion under such conditions could then cause individuals to form more exclusive associations with fewer other individuals from their community. But why would giraffes venture near to bomas at all? Previous research on the same population observed that adult female groups with calves were more likely to be closer to bomas than groups without calves (Bond, Lee, Ozgul, & König, 2019), possibly due to significantly lower predator densities on village lands compared with protected areas (Lichtenfeld, 2005). Female giraffes may therefore face a trade-off between maintaining cohesion within their social community and reducing predation risk to their calves. Although in the current study we did not detect an effect of distance to towns on relationship strength or social exclusivity, a previous study found that adult females have larger home ranges when living closer to towns (Knüsel, Lee, König, & Bond, 2019). We documented the closest observation of a giraffe group to a town was 0.35 km, and the next-closest distance of a group was 1.01 km. In contrast, the closest group to a boma was 0.02 km, and we recorded 289 groups within 1.01 km of a boma. Because adult females

appear to avoid towns altogether, there was no meaningful variation in distance to such large settlements among communities and we could not detect an influence of proximity to towns on social structure.

Our results suggest an indirect effect of human presence on megaherbivore social structure that reflects recent findings of various effects of anthropogenic disturbances on social structure in a diverse range of taxa. Hyenas living in areas of a national park with higher levels of human activity had less dense social networks, indicating animals interacted less with other clan members (Belton, Cameron, & Dalerum, 2018). Giraffes in a population with high levels of tourism and a high density of lions appeared to have weaker associations and more exclusive relationships than in a population without lions and few tourists (Muller, Cuthill, & Harris, 2019). The results of that study, while remaining unclear due to a lack of statistical support, do align with our theory-driven predictions, and our findings, that disturbances can disrupt social structure. In a key experimental study, induced social instability (temporarily splitting otherwise stable groups) resulted in more exclusive, but overall weaker relationships among members of zebra finch colonies. This change in social structure then adversely affected collective actions, such as foraging efficiency (Maldonado-Chaparro, Alarcon-Nieto, Klarevas-Irby, & Farine, 2018). In our study, we found that variation in social structure of giraffe communities along a gradient of human presence matched exactly the predictions of the zebra finch study, with the members of communities living closer to bomas having weaker relationship strengths and more exclusive social associations. In giraffes, functionally important collective actions might involve making decisions about movements (Berry & Bercovitch, 2015), synchronising activities across larger groups (Muller, Cantor, Cuthill, & Harris, 2018), and sharing care of young (Langman, 1977). If changes in social relationships translate to decreased effectiveness in performing these

collective actions, then proximity to traditional human settlements could, indirectly, have negative effects on fitness.

Social stability, and the patterns of social connections among members of a group or community, have demonstrable and measurable consequences across a spectrum of group-living animals. The number of both weak and strong associations between female chacma baboons (*Papio ursinus*) influences fitness, with more strong associations predicting birth rate and more weak associations predicting infant survival and longevity (McFarland et al., 2017). For female savanna baboons (*Papio cynocephalus*), adverse social circumstances in early life can significantly increase social isolation in adulthood, and reduce adult life span (Alberts, 2019). Adult rock hyraxes (*Procavia capensis*) that live in groups with more equal associations live longer (Barocas, Illany, Koren, Kam, & Geffen, 2011). Social integration among female horses increases foal birth rates and survival, and decreases harassment by males (Cameron, Setsaas, & Linklater, 2009). Experimentally induced chronic social instability alters alloparental care, and increases anxiety in female rodents and their offspring (Ebensperger et al., 2017; Pittet, Babb, Carini, & Nephew, 2017). In our study we find that proximity to traditional human settlements in a wild mammal population is correlated with the signatures of social systems that have experienced repeated disruptions resulting in instability (Maldonado-Chaparro, Alarcon-Nieto, Klarevas-Irby, & Farine, 2018).

Our study also revealed that giraffes can form distinct social communities within a larger-scale metapopulation. The partitioning of the metapopulation into discrete communities with relatively high modularity, meaning female giraffes associated with each other much more frequently within than between the communities, indicates clear social clustering even among individuals that share the same space. Multiple scales of social organization were documented in a population of reticulated giraffes (*G. c. reticulata*) in Kenya (VanderWaal, Wang, McCowan,

Fushing, & Isbell, 2014), where females exhibited the strongest social associations within a core group and maintained moderate associations with other members of their community, but had low association rates between their two identified communities. However, these two communities were geographically separated by a river. In our metapopulation, the presence of a lake and substantial geographical distance also split the insular Lake Manyara National Park community from all others (Fig. 1), but the remainder of the communities showed extensive spatial overlap and yet were relatively discrete. Thus, we reveal the potential for a higher level of organisationally distinct but spatially overlapping sets of social connections beyond the 'social cliques' of giraffes as described by VanderWaal *et al.* (2014). Social structuring is evidently an important feature of wild giraffe populations, with individuals exhibiting preferred and avoided associations beyond simply utilizing common areas (Carter, Seddon, Frère, Carter, & Goldizen, 2013). Associations among individuals are likely to be important for population persistence and should be considered when developing and implementing conservation measures for giraffes such as land-use plans and translocations.

CONCLUSIONS

Megaherbivores—plant-feeding mammals that attain an adult body mass of at least 1,000 kg (Owen-Smith, 1988)—are ecological engineers that play a key role in shaping the vegetation of African savanna ecosystems (Dublin, Sinclair, & McGalde, 1990; Palmer et al., 2008; Waldram, Bond, & Stock, 2008). Despite their ecological importance, populations of giraffes and the other two terrestrial African megaherbivores elephants and rhinoceroses, have declined precipitously over most of the continent (Ripple et al., 2015). The main direct threats to the largest herbivores are overhunting for meat and body parts, and eliminating habitat through deforestation and land cultivation (Ripple et al., 2015), but scientists still lack a fundamental

understanding of how natural and anthropogenic factors affect social structures of wild populations. The social network approach that we used for giraffes, and our methods for statistical inference about the relationship between community social structure and natural and human influences, offers a framework for examining social structure under different environmental conditions, so that network structure of populations can be compared across a gradient of interest. Using this framework, we provide evidence for disruption of social structure by humans. We recommend that future studies examine this subtle yet potentially far-reaching effect on other social species, and explore how social structure might influence fitness in wild populations.

Supplementary Materials

SELECTION OF DATASET AND ASSOCIATION INDEX

We thresholded out individuals that were rarely detected during the course of the 6-yr study because we were unable to account for differences in their detectability, and in social network analysis is it preferable to have missing nodes rather than inaccurate edges (Farine & Whitehead, 2015). Whitehead (2008b) recommended constructing networks using individuals identified in at least five sampling periods, and to apply sequentially larger minimum thresholds to determine whether results changed substantially as individuals with fewer detections are excluded. We restricted our dataset for network construction to animals detected $\geq$ 6 times, as this cutoff was used in previous analyses of giraffe social networks (Carter, Brand, Carter, Shorrocks, & Goldizen, 2013; Carter, Seddon, Frère, Carter, & Goldizen, 2013; VanderWaal, Wang, McCowan, Fushing, & Isbell, 2014). However, we wanted to maximise the accuracy of our edge weights while still balancing the need to include an adequate sample of nodes to represent the network as realistically as possible, therefore we also constructed networks for

individuals seen in $\geq$ 8 and $\geq$ 10 sampling events and evaluated the consistency of edge weights and community detection (Table S1) as we implemented the sequentially larger observational thresholds (e.g., Cantor et al., 2012; Tavares, Samarra, & Miller, 2017). We quantified the mean/SD edge weights and non-zero mean/SD edge weights among the three observational thresholds (Whitehead, Bejder, & Ottensmeyer, 2005; Table S1).

Edges in proximity networks are defined using an association index, which is proportional to the rate of association, or the proportion of times individuals were observed together versus apart (Farine & Whitehead, 2015). One biological definition of the weights of edges is the probability that two individuals were observed together given that at least one was observed during the sampling period, known as the simple ratio index (SRI). SRI is expressed as $E_{AB} = \frac{x}{(x+y_{AB}+y_A+y_B)}$, where the edge weight (E) between individuals A and B is the number of sampling periods where they co-occurred (x) divided by the number in which one or both were identified: (y_{AB}) is the number of times both *A* and *B* were observed in the same sampling period but not together, (y_A) is the number of sampling periods where only *A* was seen, and y_B is the number of samples where only *B* was seen (Farine & Whitehead, 2015). The SRI produces edge weights that capture the association rate. We photo-captured an annual mean of 490 giraffes from 578 groups, and in the same annual time frame we knowingly failed to photograph a mean of 23 giraffes (4.7% of individuals per year) within 10 different groups (1.7% of groups per year). We likely occasionally missed other individuals deeply hidden in vegetation, but our rate of photo-capture was relatively high for individuals we knowingly detected. However, our sampling period of approximately 10 days was relatively long and each giraffe was viewed for only a small proportion of the sampling period, thus each individual most likely had other associates during the rest of the sampling period when we did not monitor the individual (Whitehead, 2008b). In this case y_A and y_B might be biased upward and x biased downward,

lowering the association rate. When individuals are identified more when apart, as was likely for our sampling design, the half-weight index (HWI) was designed to correct for at least some of the bias in the SRI. The HWI is defined as $E_{AB} = \frac{x}{(x+y_{AB}+\frac{1}{2}(y_A+y_B))}$. Most other social network analysis studies of giraffes that utilised data collected from capture-mark-recapture studies used HWI (Carter, Brand, Carter, Shorrocks, & Goldizen, 2013; Carter, Seddon, Frère, Carter, & Goldizen, 2013; Muller, Cantor, Cuthill, & Harris, 2018; Wolf, Ngonga Ngomo, Bennett, Burroughs, & Ganswindt, 2018; but see VanderWaal, Wang, McCowan, Fushing, & Isbell, 2014). However, the HWI is based on an arbitrary rate of missing observations and when that arbitrary rate is not true the HWI does not result in a better approximation of association rates when compared to SRI. We generated edge weights using both SRI and HWI and compared results. As expected, mean edge weights were lower using SRI, but non-zero mean edge weights were the same (Table S1). We also performed community detection using both SRI and HWI and compared results (Table S1). Hoppitt and Farine (2018) recommended using SRI when no calibration data about incomplete observations are available. Thus for further analyses we used the SRI with the dataset of individuals seen $\geq$ 6 occasions.

ROBUSTNESS OF OBSERVED NETWORK

We used methods recommended by Whitehead (2008a) to explore how well our observed metapopulation network reflected "real" patterns. To assess whether our matrix of association indices among giraffes was sufficient for describing giraffe social structure, we calculated the correlation between the true association indices and the estimated association indices (*r*) using formulas and procedures in SocProg 2.8 (Whitehead, 2016). The Pearson's correlation coefficient *r* is an indicator of the power of the analysis to detect the true social system (accuracy of the observed association matrix relative to the estimated association matrix), with *r* values

close to 1 indicating a good representation and values around 0.4 indicating a moderate representation (Whitehead, 2016). We estimated standard errors for *r* from bootstrapping with 100 replicates.

The Pearson's correlation coefficient *r* between true and estimated association indices—a measure of the power of the analysis to detect the true social system—was 0.569 (SE = 0.028), suggesting a better-than-moderate representation of the social structure of our giraffe metapopulation (Whitehead, 2008a; 2016).

ENVIRONMENTAL AND SOCIAL PREDICTORS

To generate environmental and social predictors of social structure, we plotted all giraffe group locations on a GIS using ArcMap 10.5.1 (Environmental Systems Research Institute, Redlands, CA, USA). We calculated 95% kernel home ranges using locations from all individuals in each community with the package *adehabitatHR* in R (Calenge, 2006). We derived vegetation type in our study area from an existing potential natural vegetation map developed by the University of Copenhagen's Vegetation and Climate Change in Eastern Africa (VECEA) project (Kindt et al., 2011). To calculate proportion of volcanic soil grasslands in the community home ranges we used the function "intersect" in package *raster* for R (Hijmans & van Etten, 2012). We used Google Earth imagery to map all bomas and towns. To calculate distances to bomas and towns we used the "Generate Near Table" function in the Analysis Tools toolbox in ArcMap™.

Table S1. Summary of the edge weights (± SD) from networks of adult female giraffes in the Tarangire Ecosystem, northern Tanzania, 2011–2016, using three different observational thresholds and two association indices (SRI = simple ratio index, HWI = half-weight index). Associations were assumed by gambit of the group. Observation thresholds included adult females seen ≥ 6, ≥ 8, and ≥ 10 times over 31 surveys (1 detection per survey). Number of communities and modularity *Q* generated from four algorithms (CEB = Community Edge Betweenness, CFG = Cluster Fast Greedy, LEC = Leading Eigenvector Community, and CW = Cluster Walktrap) using package *igraph* for R. Bolded are highest modularity *Q* of the four algorithms.

Observation Threshold (number of observations per individual)	≥6	≥8	≥10
Number of individuals in dataset	540	414	328
Number of groups in dataset	1944	1751	1571
Simple Ratio Index (SRI)			
Mean±SD SRI	0.004 ± 0.022	0.0052 ± 0.0238	0.0063 ± 0.0263
Non-Zero Mean±SD SRI	0.058 ± 0.234	0.0690 ± 0.2534	0.0848 ± 0.2786
Number of Communities and Modularity *Q*			
CEB	16	6	5
Q	0.709	0.687	0.668
CFG	7	6	**6**
Q	0.712	0.686	**0.678**
LEC	10	8	6
Q	0.681	0.683	0.653
CW	**14**	**15**	10
Q	**0.741**	**0.795**	0.675
Half-Weight Index (HWI)			
Mean±SD HWI	0.008 ± 0.038	0.0093 ± 0.0409	0.0113 ± 0.0451
Non-Zero Mean±SD HWI	0.058 ± 0.234	0.0690 ± 0.2534	0.0848 ± 0.2786
Number of Communities and Modularity *Q*			
CEB	20	**15**	5
Q	0.698	**0.698**	0.670
CFG	7	6	5
Q	0.696	0.687	0.670
LEC	11	9	5
Q	0.677	0.687	0.670
CW	**14**	16	**10**
Q	**0.732**	0.696	**0.670**

Table S2. Local giraffe population density, relationship strength and social exclusivity, proportion of volcanic soil grasslands, and distance to bomas and towns for 11 communities of adult female Masai giraffes in the Tarangire Ecosystem, Tanzania, 2011–2016.

	Population Density of Community				Relationship Strength and Social Exclusivity								Vegetation	Human Influence	
Community	#AFs/ nodes[1]	HR km[2]	#AFs in HR	PopDen[2]	Mean EW[3]	SD EW	*P*[4]	Mean >0 EW[5]	SD >0 EW	EW CV[6]	Mean random EW CV[7]	*P*[8]	Prop_gv[9]	Dist_boma[10]	Dist_town[11]
1	34	448.78	286	0.64	0.033	0.058	0.000	0.332	0.471	1.748	1.480	0.0001	0.03	4.67	22.16
2	59	142.39	81	0.57	0.067	0.081	0.000	0.616	0.486	1.199	0.741	0.0000	0.00	11.23	12.74
3	14	170.05	187	1.10	0.078	0.096	0.005	0.561	0.498	1.234	0.930	0.0002	0.00	11.39	30.67
5	47	320.64	428	1.33	0.034	0.054	0.000	0.409	0.492	1.568	1.247	0.0000	0.03	8.70	16.16
6	61	134.92	287	2.13	0.033	0.047	0.018	0.470	0.499	1.419	1.195	0.0000	0.86	3.10	5.63
7	70	228.15	312	1.37	0.019	0.035	0.000	0.316	0.465	1.814	1.512	0.0000	0.48	2.06	6.06
8	40	211.77	247	1.17	0.046	0.059	0.028	0.514	0.500	1.296	1.072	0.0000	0.00	12.19	26.08
9	28	278.37	288	1.03	0.039	0.052	0.033	0.518	0.500	1.327	1.046	0.0000	0.55	2.22	9.92
10	55	120.71	272	2.25	0.041	0.051	0.003	0.539	0.499	1.264	1.055	0.0004	0.71	3.24	3.90
13	53	253.51	405	1.60	0.052	0.060	0.006	0.614	0.487	1.167	0.950	0.0002	0.89	2.52	4.88
14	65	67.55	228	3.38	0.036	0.051	0.008	0.429	0.495	1.398	1.325	0.0004	0.00	2.98	10.78

[1] #AFs/ nodes = Number of adult females (nodes) in network (total N=540)
[2] PopDen = Number of all adult females (N=1,139) ever detected within the home range of each community, divided by the home-range size.
[3] Mean EW = Mean edge weight (association strength calculated from SRI) among all dyads in the community network.
[4] *P* = Number of times the observed mean association strength was greater than that of a randomised network, divided by 50,000.
[5] Mean >0 EW = Mean non-zero edge weight among all dyads in the community network.
[6] EW CV = Coefficient of variation of all edge weights in the observed community network.
[7] Mean random EW CV = Mean coefficient of variation of all edge weights from 10,000 randomised community networks.
[8] *P* = Number of times the observed edge weight CV was greater than the edge weight CV from a randomised network, divided by 10,000.
[9] Prop_gv = Proportion of grasslands on volcanic soils within the community home range.
[10] Dist_boma = Distance (km) of average distance between all locations of all individuals in a community to the nearest boma.
[11] Dist_town = Distance (km) of average distance between all locations of all individuals in a community to the nearest town.

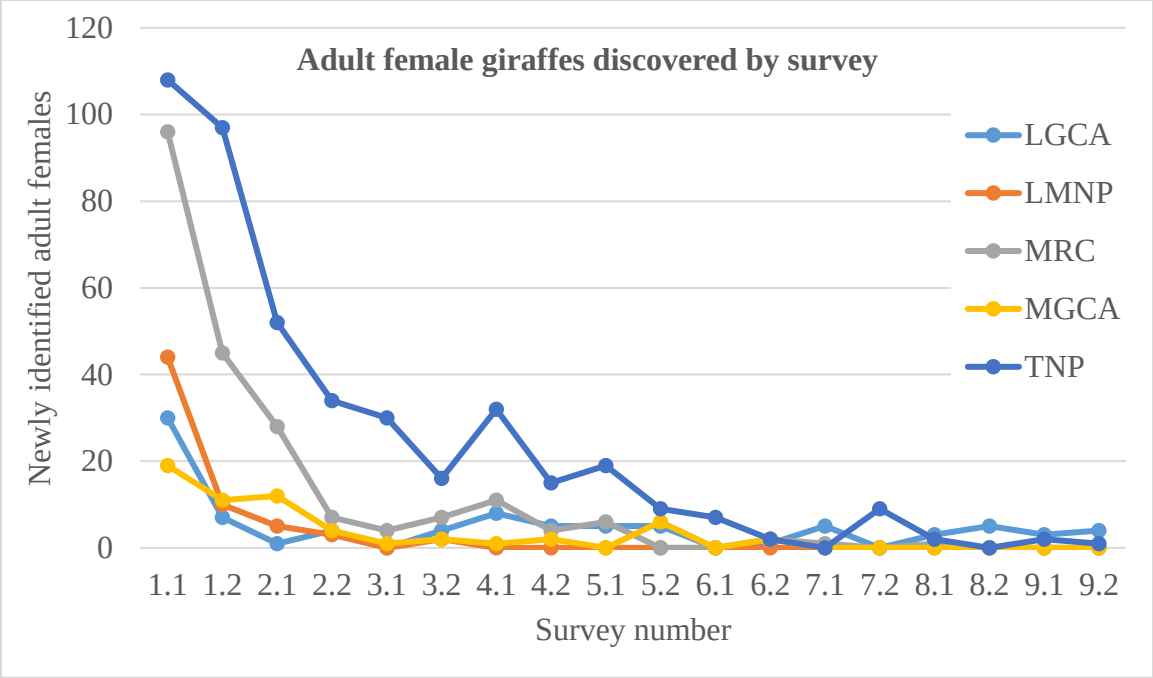

Figure S1. Number of newly identified adult female giraffes by survey, 2012 – 2014. Year 1: surveys 1.1 – 3.2. Year 2: surveys 4.1 – 6.2. Year 3: surveys 7.1 – 9.2. Of the total adult females identified in the first 3 years of the study, 80% were discovered in 2012, 16% were discovered in 2013, and 4% were discovered in 2014.

Chapter 3

Drivers of life-history variation in a giraffe metapopulation: the role of environmental versus social factors

Monica L. Bond · Barbara König · Arpat Ozgul · Damien Farine · Derek E. Lee

Submitted to Journal of Animal Ecology

Abstract Population demographic rates can be influenced by both environmental and social processes. However, populations are typically defined as spatially contiguous sets of individuals, making it difficult to partition the relative contributions of environmental and social effects. In some species, such as the Masai giraffes of Tanzania, individuals live in distinct social communities that overlap with others, allowing us to overcome this limitation and explore social and environmental drivers of life-history variation. We considered social communities to be subpopulations, and tested for variation among 10 subpopulations in adult female survival, calf survival, and reproductive rate (calf to adult female ratio). We then related variation in demographic rates to differences among subpopulations in vegetation, proximity to two types of human settlements, local giraffe population density, and social metrics of relationship strength and exclusivity among adult females. We found that demographic rates were correlated with vegetation and anthropogenic factors, but not with factors associated with social relationships among females. Subpopulations with more dense bushlands in their ranges had lower calf survival probabilities, and those closer to human settlements had higher reproductive rates, likely due to spatial differences in natural predation. Calf survival probabilities also were greater in subpopulations with higher local adult female densities. By contrast, we did not find any among-subpopulation effects on adult female survival. Our approach of comparing demography among spatially overlapping yet distinct social communities provides a deeper understanding of

environmental versus social drivers of fine-scale demographic variation and can be used to craft targeted conservation measures for at-risk species.

Keywords capture-mark-recapture, social network analysis, population biology, demography, giraffe, *Giraffa camelopardalis*

Introduction

Survival and other demographic traits of a species can differ markedly among populations (Coulson, Albon, Pilkington, & Clutton-Brock, 1999; Paradis et al., 2000; Frederiksen, Harris, & Wanless, 2005; Lee, Bond, Kissui, Kiwango, & Bolger, 2016; Lee & Bolger, 2017). Demographic rates can be influenced by both environmental (Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toïgo, 2000; Nilsen et al., 2009; Contasti, Tissier, Johnstone, & McLoughlin, 2012) and social processes (Wey & Blumstein, 2012; Blumstein, 2013) and their interactions, and these processes can operate at various scales (Grosbois et al., 2009). Identifying which demographic parameters differ among populations, and why they differ, is therefore fundamental to understanding population ecology. Investigating potential links among the environment, sociality, and demography requires long-term, large-scale studies, because such studies are more likely to include contrasting environmental and social conditions (Clutton-Brock & Sheldon, 2010).

To explore the potential factors that influence demographic parameters, it is essential to first objectively define populations or subpopulations in continuous space (Coulson, Albon, Pilkington, & Clutton-Brock, 1999; Schaefer, 2006; Harwood, 2009). Wells and Richmond (1995) proposed that a population be defined as a group of individuals demonstrating a clear disjunction from others groups in spatial, genetic, and/or demographic structure, but appropriate boundaries are often difficult to recognize (Thomas & Kunin, 1999; Zannèse et al., 2006). Large

populations oftentimes are comprised of discrete social communities of individuals that regularly interact with each other more than they interact with individuals in other communities (e.g., Lusseau et al., 2006; Cantor et al., 2012; VanderWaal, Wang, McCowan, Fushing, & Isbell, 2014). Such social communities give rise to population structure through preferences in social associations, as opposed to discrete space use. Some distinct social communities may overlap substantially in space, with individuals of different communities sharing the same areas but rarely observed together (Bond, König, Lee, Ozgul, & Farine, in revision) or forming supergroups that split back up into their distinct group or community (Papageorgiou et al., 2019). These socially defined subpopulations could potentially allow us to better understand the drivers of variation in demographic rates because they share many of the same environmental conditions.

The adult female Masai giraffe (*Giraffa camelopardalis tippelskirchi*) population in the Tarangire Ecosystem (TE) of Tanzania consists of more than a dozen discrete social communities, each overlapping in space use with other communities (Bond, König, Lee, Ozgul, & Farine, in revision). Giraffes are long-lived (up to 30 yr), large (800–1200 kg), iteroparous with non-seasonal birth flow reproduction, browsing ruminants that eat leaves, twigs, and fruits of woody savanna vegetation in sub-Saharan Africa (Dagg, 2014). Within communities, giraffe group formations merge and split in a fission-fusion process (Aureli et al., 2008), but adult females show significant preferred and avoided associations with other females (Carter, Seddon, Frère, Carter, & Goldizen, 2013; Carter, Brand, Carter, Shorrocks, & Goldizen, 2013; VanderWaal, Wang, McCowan, Fushing, & Isbell, 2014; Bond, König, Lee, Ozgul, & Farine, in revision), and females with preferred relationships are more closely related than those that appear to avoid each other (Bercovitch & Berry, 2012; Carter, Seddon, Frère, Carter, & Goldizen,

2013). The resulting association patterns form a structured social network characterized by multiple levels of organization (VanderWaal, Wang, McCowan, Fushing, & Isbell, 2014; Bond, König, Lee, Ozgul, & Farine, in revision). Previous demographic analyses of giraffes in this study area found adult female and calf survival and reproductive rates varied among spatially discrete administrative areas (Lee, Bond, Kissui, Kiwango, & Bolger, 2016; Lee & Bolger, 2017), but demographic variation among the socially defined, overlapping communities is unknown. Further, no studies have as yet examined the influence of social factors on giraffe demography.

Here we analyse individual-based photographic capture-recapture data from more than 1,400 adult females and calves in 10 subpopulations defined by social community membership (Fig. 1). The TE is a large, unfenced, heterogeneous study area with diverse vegetation types, two national parks and a private ranch, and areas of human settlements. Such habitat heterogeneity, combined with the clear community structure in giraffes, provide an opportunity to examine whether variation in demographic rates arises as functions of environmental or social factors. We first estimated variation among the subpopulations in demographic rates of adult female survival, calf survival, and calf to adult female ratio. We then explored the relative influences of vegetation, anthropogenic, and social factors on among-subpopulation variation in demographic rates, basing our predictions on previous research in this study metapopulation. Our large sample size as well as the environmental heterogeneity, connectedness, and large scale of our study area allowed us to consider multiple social communities as subpopulations for demographic analysis. The framework of comparing demography among overlapping socially defined subpopulations represents a novel approach to disentangling potential environmental and social factors that might drive population dynamics.

Methods

FIELD DATA COLLECTION

Our study area is in the core of the Tarangire Ecosystem, where we sampled 1,500 km^2 in five administrative areas with differing management activities (Fig. 1). We conducted 30 daytime, fixed-route road transect surveys for giraffes between January 2012 and October 2016, plus a pilot survey during May–June 2011. We photographed and later identified individual giraffes throughout the study area using coat patterns unique to each animal (Foster, 1966). Details of the study area and field data collection are in Supplementary Materials.

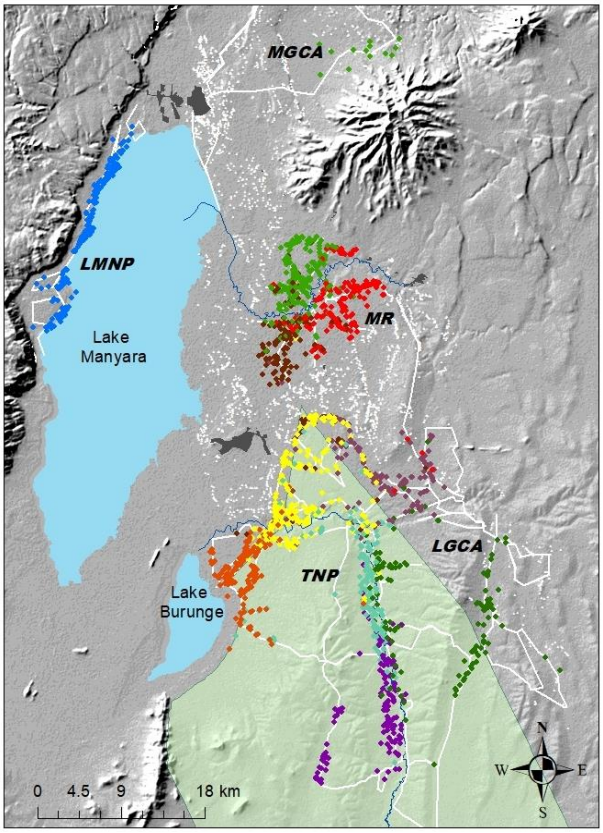

Figure 1. Locations of 10 socially defined subpopulations (communities) of 512 adult female Masai giraffes in the Tarangire Ecosystem of northern Tanzania, 2011–2016. Subpopulations of socially associated individuals were delineated with the cluster-walktrap algorithm. LMNP is Lake Manyara National Park, TNP is Tarangire National Park, MR is Manyara Ranch, MGCA is Mtowambu Game Controlled Area, and LCGA is Lolkisale Game Controlled Area. White lines are tracks surveyed for giraffe groups, blue lines are rivers, white points are bomas, dark grey polygons are towns, and green polygon is TNP.

DATA ANALYSIS

We analysed data from adult females and not adult males in this study because (1) adult females make up the reproductively relevant segment of polygynous vertebrate populations where sex ratios are not very male-biased (Rankin & Kokko, 2007); (2) most population modelling in such systems only consider females (Caswell, 2002); and (3) adult female giraffes show stronger preferences in their associations, and form longer-term associations with other females than do adult males and subadult females (Bercovitch & Berry, 2012; Carter, Seddon, Frère, Carter, & Goldizen, 2013; Carter, Brand, Carter, Shorrocks, & Goldizen, 2013).

There are now numerous methods for partitioning a social network into communities based on features such as statistically higher association rates within than among communities (reviewed by Porter, Onnela, & Mucha, 2009 and Fortunato, 2010). We constructed social networks by generating an association matrix of pairs of adult females using the simple ratio index. We then ran a community detection algorithm on the network, and delineated more than a dozen social communities (subpopulations) based on the associations. See Supplementary Materials for details on creating our dataset, analysing social networks, and delineating communities.

For our demographic analyses, we: (1) created encounter histories for individual adult females and calves; (2) assigned individuals to one of the subpopulations; (3) estimated subpopulation-specific demographic rates of adult female survival, calf survival, and calf to adult female ratio and tested for significant variation among subpopulations; and (4) analysed environmental and social covariates of subpopulation-specific variation in demographic rates. The final dataset contained encounter histories for giraffes in 10 subpopulations spanning the entire study area, including 684 adult females (mean = 68 per subpopulation, range = 27–93) and 744 calves (mean = 74 per subpopulation, range 43–133) for estimating reproductive rates, and 672 adult females (mean = 67 per subpopulation, range = 26–93) and 732 calves (mean = 73 per subpopulation, range = 43–133) for estimating seasonal apparent survival rates. These data included 75% of all known adult females and 80% of all known calves identified in our metapopulation over the 6-year study period.

Estimating Demographic Rates—

Survival: To analyse seasonal adult female apparent survival and seasonal calf apparent survival, we created individual encounter histories for analysis in Program MARK 8.2 (White &

Burnham, 1999). We utilized Pradel robust design models to estimate apparent survival (S), temporary emigration (γ'' and γ'), and capture and recapture probabilities (p and c) (Pradel, 1996; Nichols, Hines, Lebreton & Pradel, 2000). We used standard notation for models where parameters had subpopulation-specific (group) values (g), temporal variation (t), or constant equal parameter values (.). We began with the most fully parameterized model in our set with subpopulation effects on survival {S(g)}, subpopulation effects on temporary emigration {γ''(g) and γ'(g)}, and with both temporal and subpopulation effects in capture rates {p(g*t)} and recapture {c(g*t)} rates. We were unable to conduct surveys in Lake Manyara National Park during the last two primary sampling periods in 2016 due to logistical constraints, so during all analyses we fixed p and c parameters to zero for that subpopulation for those two primary sampling periods.

Before modelling our parameter of interest which was survival, we ranked simpler models of capture probability {p(.)}, {p(g)}, {p(t)}, {p(g+t)}, and recapture probability {c(.)}, {c(g)}, {c(t)}, {c(g+t)}. We also ranked a simpler constant model of temporary emigration {γ''(.) and γ'(.)}, and we considered a group covariate model where temporary emigration varied with the distance of each subpopulation from the edge of the study area {γ''(dist) and γ'(dist)}. After selecting the best model of nuisance parameters, we ranked models of survival that differed by subpopulation {S(g)}, constant survival among subpopulations {S(.)}, and survival as a function of five environmental and two social covariates (see below for details).

Throughout model ranking and selection procedures, we used logit link functions and 2nd part estimation. For model comparison, we used Akaike's Information Criterion corrected for small samples (AIC_c) and AIC_c weights in an information-theoretic approach (Burnham & Anderson, 2002). We considered models with AIC_c <2 to be competitive, and we examined the

signs of the beta coefficients to determine the direction of the covariate effects. We investigated the significance of the covariate effects by comparing the difference between AIC_c of the covariate model with the constant model. There is no goodness-of-fit test of whether the most general Pradel model in our candidate model set adequately fits the data for robust design (Cooch & White, 2019). Therefore, to test goodness-of-fit, we combined our two secondary survey samples from our robust design into a simple binary variable (seen, not seen) and treated the resulting encounter history as a live-encounter Cormack-Jolly-Seber (CJS) model (Cooch & White, 2019). We then tested the fit of our data to the fully-time-dependent CJS model using program RELEASE TEST 2 + TEST 3 (Burnham, Anderson, White, Brownie, & Pollock, 1987) and corrected for any overdispersion using median ĉ (Cooch & White, 2019).

Reproductive rate: Giraffe calves form crèches and in the field it is not possible to attribute a calf to its mother unless extended suckling behaviour is observed. Therefore, we were unable to calculate individual adult female reproductive effort and instead estimated subpopulation-level reproductive rates as an annual ratio of calves to adult females. For the ratio numerator, we needed to account for imperfect detection of neonatal giraffe calves, as well as for calf mortality between birth and the first observation of the calf during surveys (Lee, Bond, Kissui, Kiwango, & Bolger, 2016). We corrected the calf count for imperfect detection and survival from birth to first observation by first dividing the raw calf count by the subpopulation-specific capture probability (p) estimated using the top-ranked model of calf survival, and then dividing again by the square root of the subpopulation-specific calf survival probability (S) from the top-ranked model (assuming calf births were evenly distributed throughout the season before first detection). We then divided the corrected calf count by number of survey years for the

subpopulation and multiplied by 10. The ratio denominator was the total number of adult females enumerated in each subpopulation, multiplied by 10. The final reproductive rate equation was:

$$\frac{\text{Corrected count of calves in subpopulation} \times 10}{(\text{Number of years subpopulation was surveyed}) \times (\text{Count of adult females} \times 10)}$$

We modelled variation in reproductive rate with logistic regression (glm) using a binomial error distribution (link=logit) with the ratio of calves ("successes") per adult female ("failures") in each subpopulation as the response. To determine which subpopulation reproductive rates differed significantly from each other, we conducted pairwise post-hoc Tukey's multiple comparison tests using package *multcomp* (Bretz, Hothorn, & Westfall, 2010) in R (R Core Development Team, 2019). We conducted model selection for reproductive rate using package *MuMIn* (Bartoń, 2019) and *AICcmodavg* (Mazerolle, 2019) in R. We tested for overdispersion using a goodness-of-fit test. We adjusted for lack-of-fit by using a quasi-binomial distribution (family=quasibinomial), and including ĉ (Pearson Chi-square residuals / residual degrees of freedom) in our model selection process (Venables & Ripley, 2002). As with survival, we followed an information-theoretic approach to rank a priori models, with AIC_c or quasi-AIC_c, depending on whether overdispersion was present in the data. We back-transformed the linear predictor from logits (z) to proportions using $p = 1/[1 + 1/\exp(z)]$ to present the odds ratios for covariate effects.

Environmental and Social Covariates—To understand why demographic rates might differ among subpopulations, we modelled the effects of seven covariates on seasonal adult female apparent survival, seasonal calf apparent survival, and reproductive rate. (1) Proportion of dense bushlands in the subpopulation's home range: $S(bush)$. (2) Proportion of grasslands on volcanic soils in the subpopulation's home range: $S(volc)$. (3) Distance (in km) from the centre of the subpopulation's home range to the nearest town: $S(town)$. (4) Distance (in km) from the

centre of the subpopulation's home range to the nearest boma: *S*(*boma*). Permanent settlements (towns) are clusters of concrete structures, whereas Masai homesteads (bomas) comprise one or more temporary structures made of natural materials such as wood, mud, and grass, and are encircled by fencing of cut thorny branches. Towns are densely populated areas inhabited by bushmeat poachers, whereas bomas are inhabited by pastoralist Masai tribespeople who typically do not kill wild animals for meat. Small agricultural plots occur near permanent settlements, but most vegetation in the study area consists of natural, uncultivated lands. (5) Local giraffe population density, which included all adult female giraffes ever detected within the home range of the subpopulation, regardless of number of detections or subpopulation membership or whether they were subadults at the beginning of the study period (N=1,139 adult females): *S*(*dens*). (6) Average relationship strength between associated pairs of females in each subpopulation, measured as non-zero edge weight, with higher values suggesting females are on average associating with a larger number of other females (Whitehead, 2008): S(*ew*). (7) Exclusivity of relationships in each subpopulation, measured as the coefficient of variation of edge weights, with higher values indicating females have stronger relationships with some and weaker relationships with others within their subpopulation (Farine & Whitehead, 2015): S(*ewcv*). See Supplementary Materials for details about calculating environmental covariates.

Based on previous research, we predicted adult female survival would increase with increasing distance from areas of intensive human influences (towns) where poaching is prevalent, but be relatively unaffected by bomas (Lee, Bond, Kissui, Kiwango, & Bolger, 2016; Knüsel, Lee, König, & Bond, 2019). In contrast, calf groups in our study area were more likely to occur closer to bomas and in bushland vegetation (Bond, Lee, Ozgul, & König, 2019) so we predicted higher calf survival and reproductive rates in those areas. Volcanic soils are

particularly fertile, which may enhance forage quality (Hansen, Mugambi, & Bauni, 1985), and the administrative area with the most volcanic soil grasslands (Manyara Ranch) had the highest reproductive rate in a previous study (Lee, Bond, Kissui, Kiwango, & Bolger, 2016), so we expected that a greater proportion of these grasslands in a subpopulation's home range would be correlated with higher calf survival and reproductive rates.

Earlier social analyses of this population found weaker relationship strength and greater social exclusivity among females in subpopulations closer to bomas, and we suggest these social metrics indicate a disrupted social environment (*sensu* Maldonado-Chaparro, Alarcon-Nieto, Klarevas-Irby, & Farine, 2018). Here we predicted that subpopulations with weaker relationship strengths and greater social exclusivity would have lower adult and calf survival probabilities as a result of disruption to the social structure. Finally, we expected adult female survival and calf survival would be higher in subpopulations with higher local giraffe population density, as we presume more adult females in an area could better detect predators, and/or females might congregate with their calves and fare better in areas of better-quality habitat. Table 1 shows location in the study area, number of adult females and calves, calf survival and reproductive rates, and environmental and social covariate values for each subpopulation. We did not include explanatory variables together in the same model, but we tested for and report multicollinearity among explanatory variables by calculating Spearman's correlation coefficients (see Supplementary Materials and Table S1).

Table 1. Sample sizes, years of study, calf survival and reproductive rates, and social and environmental covariates for 10 socially defined subpopulations of adult female Masai giraffes and calves in the Tarangire Ecosystem, northern Tanzania, 2011–2016.

Location	Number adult females	Number calves	Years	Calf survival probability (*S*)	Repro-ductive Rate	Mean >0 Edge Weight	Mean Edge Weight CV	Local giraffe density	Distance to boma (km)	Distance to town (km)	Proportion volcanic grassland	Proportion bushlands	Distance to edge (km) for γ
SSE TNP/LGCA	62	43	5	0.90	0.42	0.33	1.75	0.64	4.67	22.16	0.03	0.39	7.6
LMNP	64	59	4	0.91	0.45	0.62	1.20	0.57	11.23	12.74	0.00	0.30	1
Central TNP	62	57	5	0.92	0.46	0.41	1.57	1.33	8.70	16.16	0.03	0.22	10
N MR/MGCA	84	79	5	0.94	0.51	0.47	1.42	2.13	3.10	5.63	0.86	0.00	4.5
NNW TNP	70	133	5	0.92	0.88	0.32	1.81	1.37	2.06	6.06	0.48	0.17	2
SW TNP	65	53	5	0.88	0.42	0.51	1.30	1.17	12.19	26.08	0.00	0.49	8
NNE TNP/LGCA	27	45	5	0.92	0.92	0.52	1.33	1.03	2.22	9.92	0.55	0.16	4
SE MR	77	110	5	0.94	0.80	0.54	1.26	2.25	3.24	3.90	0.71	0.01	5.6
SW MR	80	88	5	0.93	0.57	0.61	1.17	1.60	2.52	4.88	0.89	0.05	4.8
W TNP	93	77	5	0.94	0.51	0.43	1.40	3.38	2.98	10.78	0.00	0.00	3.7

Results

We found substantial spatial overlap of giraffe subpopulation home ranges. Each subpopulation home range was overlapped by an average of four other subpopulation home ranges. On average, the maximum proportion one subpopulation's home range was overlapped by another was 0.44, with two subpopulations sharing >60% of their space with another. Western Tarangire National Park's subpopulation shared very little space with other subpopulations (mean = 0.08 and maximum = 0.15 overlap with 4 other subpopulations) and Lake Manyara National Park's subpopulation was spatially completely isolated from the other subpopulations. Supplementary Materials Table S2 shows all overlap values among all subpopulations.

ADULT FEMALE SURVIVAL

We found evidence for lack-of-fit in the adult female encounter history data (TEST 2 + TEST 3 $\chi^2 = 255.01$, d.f. = 82, $P < 0.001$) but median-ĉ was <3 (1.187), therefore we kept ĉ = 1.0 for model selection (Cooch & White, 2019). Our most parsimonious model included temporary emigration varying by distance to edge of the study area {S(g) γ''(dist) γ'(dist) p(g*t) c(g*t)} (Supplementary Materials Table S3).

Model selection results for seasonal adult female survival indicated that adult female survival did not vary significantly by subpopulation (Table 2). The model best supported by the data in the candidate set was constant survival across subpopulations {S(.)}(Table 2). The model of constant survival across subpopulations was 100 times better than the model with subpopulation variation in survival (model likelihood for {S(.)} = 1, and {S(g)} = 0). None of the covariate models were competitive with the top model (Table 2). Adult female seasonal apparent survival rate across all subpopulations was 0.991 (SE = 0.017, 95% CI = 0.673–0.999).

Table 2. Model selection results for constant survival, group effects, and covariate models of apparent adult female and calf survival probabilities among 10 socially defined subpopulations of Masai giraffes in the Tarangire Ecosystem, northern Tanzania, 2012–2016.

Model	AIC_c	ΔAIC_c	AIC_c Weights	Model Likelihood	Num. Par	Deviance
Adult Female Survival						
{S(.) γ''(dist) γ'(dist) p (g*t) c(g*t)}	19116.13	0.00	0.61	1.00	449	35133.59
{S(ewcv) γ''(dist) γ'(dist) p (g*t) c(g*t)}	19118.48	2.35	0.19	0.31	450	35133.58
{S(ew) γ''(dist) γ'(dist) p (g*t) c(g*t)}	19118.49	2.36	0.19	0.31	450	35133.59
{S(volc) γ''(dist) γ'(dist) p (g*t) c(g*t)}	19125.24	9.11	0.01	0.01	450	35140.34
{S(bush) γ''(dist) γ'(dist) p (g*t) c(g*t)}	19126.17	10.03	0.00	0.01	450	35141.26
{S(town) γ''(dist) γ'(dist) p (g*t) c(g*t)}	19126.45	10.32	0.00	0.01	450	35141.55
{S(boma) γ''(dist) γ'(dist) p (g*t) c(g*t)}	19127.10	10.97	0.00	0.00	450	35142.20
{S(dens) γ''(dist) γ'(dist) p (g*t) c(g*t)}	19127.27	11.14	0.00	0.00	450	35142.37
{S(g) γ''(dist) γ'(dist) p (g*t) c (g*t)}	19132.95	16.82	0.00	0.00	458	35129.13
Calf Survival						
{S(bush) γ''(.) γ'(.) p(g*t) c(g*t)}	11383.75	0.00	0.43	1.00	454	15919.17
{S(dens) γ''(.) γ'(.) p(g*t) c(g*t)}	11385.58	1.83	0.17	0.40	454	15921.00
{S(g) γ''(.) γ'(.) p(g*t) c(g*t)}	11385.97	2.22	0.14	0.33	462	15899.99
{S(boma) γ''(.) γ'(.) p(g*t) c(g*t)}	11386.32	2.57	0.12	0.28	454	15921.74
{S(volc) γ''(.) γ'(.) p(g*t) c(g*t)}	11387.13	3.38	0.08	0.18	454	15922.55
{S(town) γ''(.) γ'(.) p(g*t) c(g*t)}	11389.64	5.89	0.02	0.05	454	15925.06
{S(.) γ''(.) γ'(.) p(g*t) c(g*t)}	11389.80	6.05	0.02	0.05	453	15927.89
{S(ew) γ''(.) γ'(.) p(g*t) c(g*t)}	11391.97	8.23	0.01	0.02	454	15927.39
{S(ewcv) γ''(.) γ'(.) p(g*t) c(g*t)}	11392.41	8.66	0.01	0.01	454	15927.83

CALF SURVIVAL

For calves, we also detected evidence of lack-of-fit (TEST 2 + TEST 3 χ^2 = 121.905 d.f. = 62, $P < 0.001$), however, the median-ĉ was <3 (= 1.187), so we kept ĉ = 1.0 for model selection (Cooch & White, 2019). The best model of nuisance parameters was {S(g) γ''(.) γ'(.) p(g*t) c(g*t)} (Supplementary Materials Table S3).

The model with subpopulation-specific seasonal calf survival was better supported than the constant survival model (model likelihood for {S(g)} = 0.329, and {S(.)} = 0.049, thus 6.714

times more likely; Table 2) indicating survival varied significantly by subpopulation. Subpopulation-specific seasonal calf survival probabilities ranged from 0.88 to 0.94 (Table 1, Fig. 2). Further, the best calf survival model of the candidate set was the covariate model where survival probability varied by proportion of dense bushlands within a subpopulation's home range (Table 2). The second-ranked covariate model of local giraffe population density was competitive (ΔAIC_c = 1.833) but the top model was 2.5 times more likely (model likelihood for {*S*(bush)} = 1, and {*S*(dens)} = 0.40; Table 2).

Calf survival probability was lower with more dense bushlands in the subpopulation home range ($ß_{bush}$ = -1.401, SE = 0.464) and the 95% confidence interval did not overlap 1, indicating a significant effect (95% CI = -2.310 – -0.491). Calf survival probability was greater in subpopulations with higher local giraffe population density ($ß_{dens}$ = 0.299, SE = 0.120) and the effect was also significant (95% CI = 0.064 – 0.536).

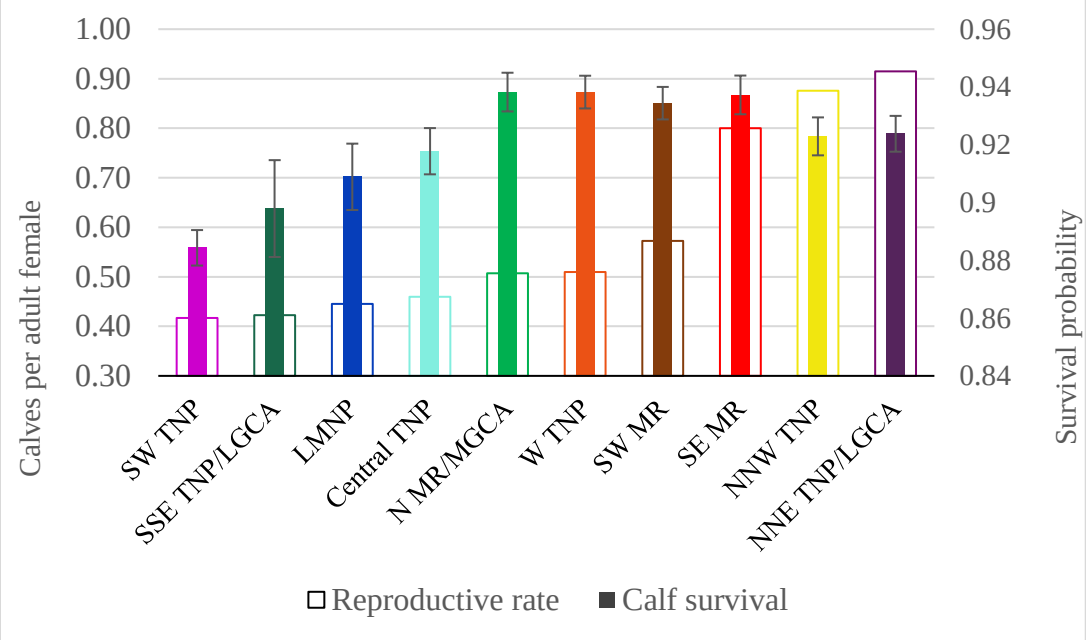

Figure 2. Reproductive rates (calves to adult females) and calf survival probabilities (±SE) for 744 calves and 684 adult female giraffes in 10 socially defined subpopulations in the Tarangire Ecosystem of northern Tanzania. Colours correspond to communities depicted in Figure 1.

REPRODUCTIVE RATE

A Tukey's multiple comparison test confirmed that most of the subpopulations varied significantly from each other in reproductive rates (Supplementary Materials Table S4, Fig. 2). We detected evidence of overdispersion in the most parameterized model ($\hat{c}$ = 7.584) so we used the quasi-binomial error distribution to test the influence of environmental and social variables on variation in reproductive rate. Model checking indicated no pattern in residuals against fitted values and the normal plot was linear. The best model included the covariate town and the coefficient was negative ($ß_{town}$ = -0.027, SE = 0.011, P = 0.033; Table 3) indicating that subpopulations farther from towns are likely to have lower reproductive rates. This model fit significantly better than a null model (χ^2 = 88.604, df = 1, P <0.0001). The odds ratio (0.973; 95% CI = 0.953–0.993) suggests that for every kilometre a giraffe community was situated farther away from the nearest town, its reproductive rate decreased by 0.03 (Fig. 3a). The covariate model with distance to boma was competitive and the coefficient also was negative ($ß_{boma}$ = -0.052, SE = 0.022, P = 0.049; Table 3). This second-ranked model also fit better than a null model (χ^2 = 78.679, df = 1, P <0.0001). The odds ratio (0.950; 95% CI = 0.909–0.991) indicates that for every kilometre a giraffe subpopulation was situated farther from the nearest boma, its reproductive rate decreased by 0.05 (Fig. 3b).

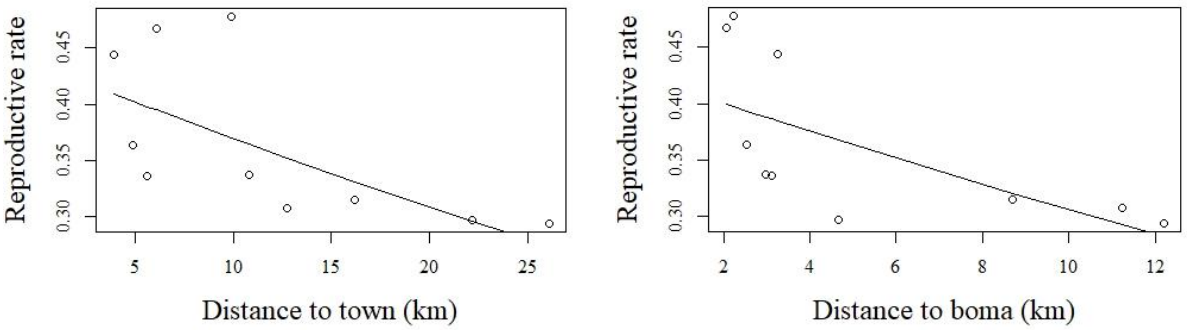

Figure 3. Predicted reproductive rate (calves to adult females) as a function of distance in km to nearest town (a) and nearest boma (b) for 10 subpopulations of socially associated adult female giraffes in the Tarangire Ecosystem of northern Tanzania, from a generalized linear model.

Table 3. Model selection results comparing general linear models of variation in reproductive rate (calves to adult females) among 10 socially defined subpopulations of Masai giraffes in the Tarangire Ecosystem, northern Tanzania. Social covariates include mean >0 edge weight and edge weight coefficient of variation. Environmental covariates include distance to nearest boma (km), distance to nearest town (km), and proportion of two vegetation types in the subpopulation home range: dense bushlands and volcanic soil grasslands.

	(Intercept)	Dense bushland	Volcanic grassland	Distance to boma	Distance to town	Edge weight	Edge weight CV	df	LogLik	$QAIC_c$	$\Delta QAIC_c$	Weight
mod_town	**-0.260**	**.**	**.**	**.**	**-0.027**	**.**	**.**	**2**	**-88.275**	**33.278**	**0.000**	**0.590**
mod_boma	**-0.302**	**.**	**.**	**-0.052**	**.**	**.**	**.**	**2**	**-93.238**	**34.587**	**1.309**	**0.307**
mod_volc	-0.710	.	0.400	.	.	.	.	2	-104.993	37.686	4.408	0.065
mod_bush	-0.439	-0.751	.	.	.	.	.	2	-114.484	40.189	6.911	0.019
mod_null	-0.552	.	.	.	.	.	.	1	-132.578	40.675	7.397	0.015
mod_ewcv	-0.855	.	.	.	.	.	0.213	2	-129.956	44.269	10.991	0.002
mod_ew	-0.396	.	.	.	.	-0.330	.	2	-131.206	44.599	11.321	0.002

Discussion

We used network analysis of social associations among hundreds of adult female giraffes in a large, free-ranging metapopulation to define socially discrete communities—here considered as subpopulations—within a heterogeneous landscape with variable vegetation and human impacts. Our aim was to elucidate key environmental or social factors that drive subpopulations dynamics within a larger metapopulation. The subpopulations were relatively discrete in terms of social associations despite substantial overlap in space use. Subpopulations exhibited variation in demography, demonstrating our ability to detect fine-scale population dynamics associated with socially mediated population structure within a large continuous metapopulation. In particular, we detected significant variation in seasonal calf survival and reproductive rates among the subpopulations, which was best explained by environmental covariates including distance to human settlements, vegetation structure, and local giraffe population density, rather than by social covariates of relationship strength and social exclusivity of the adult females.

In contrast, seasonal adult female survival was nearly constant across all subpopulations. This is not surprising, because population growth rates in long-lived animals like giraffes often are determined by variation in recruitment processes and/or fertility rates, while adult female survival remains high and constant (Gaillard, Festa-Bianchet, & Yoccoz, 1998; Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toïgo, 2000; Morris & Doak, 2002, but see Lee, Bond, Kissui, Kiwango, & Bolger, 2016). Therefore, differences in reproduction and calf survival drive variation in population dynamics among our subpopulations. When we matched socially defined subpopulations to administrative areas in the landscape, our estimates of demographic rates generally agreed with previous analyses for this population (Lee, Bond, Kissui, Kiwango, & Bolger, 2016), with lower calf survival and lower reproductive rates inside the national parks

compared to outside. However, the larger number of divisions created by social network analyses enabled finer-scaled investigation of environmental and social covariates across the landscape that highlighted specific subpopulations which had greater or lesser fitness, even within the same administrative area.

We identified less fit subpopulations with low reproductive rates and low calf survival in Lake Manyara National Park and southern Tarangire National Park (Fig. 2). These subpopulations represent a small nearly isolated national park and a portion of another larger national park. In contrast, the highest reproductive rates were documented in subpopulations in the northern part of Tarangire National Park, showing that this measure of fitness was not related to more restrictive land use or higher protection levels found in these administrative areas. Variation in reproductive output could be due to spatial variability in habitat availability or quality, food resources, weather, disease, parasites, predator pressure, human activities, and population density (e.g. Jorgenson, Festa-Bianchet, Gaillard, & Wishart, 1997; Gaillard, Festa-Bianchet, & Yoccoz, 1998; Coulson, Albon, Pilkington, & Clutton-Brock, 1999; Dhondt, 2001; Ozgul, Armitage, Blumstein, & Oli, 2006; Sanz-Aguilar et al., 2009; Contasti, Tissier, Johnstone, McLoughlin, 2012), and indeed we found environmental covariates explained variation in calf survival probabilities and reproductive rates better than a constant survival model among subpopulations. Contrary to our prediction, proportion of bushlands was correlated with lower calf survival, likely because giraffe calves are vulnerable to lion predation (Lee, Bond, Kissui, Kiwango, & Bolger, 2016) and lions prefer to hunt in dense vegetation (Hopcraft, Sinclair, & Packer, 2005). Both Lake Manyara and Tarangire national parks have substantially higher lion densities compared to outside the parks (Lee, Bond, Kissui, Kiwango, & Bolger, 2016), and within Tarangire National Park, subpopulations with higher calf survival had less

bushlands in the home range. We also found support for a model where calf survival probability increased in subpopulations with higher densities of adult female giraffes, in line with our prediction. Subpopulations closer to towns and bomas had higher reproductive rates, and we recorded the highest calf survival probabilities in the subpopulations that included Manyara Ranch with its high levels of herders and livestock, as well as in the subpopulation on the western edge of Tarangire National Park where herders also are common (Figs. 2 and 3). We therefore suspect that pastoralists disrupting natural predation is a possible mechanism for our observed spatial demographic patterns.

Calf survival probabilities were similar among spatially overlapping subpopulations, but reproductive rates differed significantly even among subpopulations with substantial overlap. As an example, 54% of the range of giraffes in the southwest Manyara Ranch subpopulation was overlapped by the southeast Manyara Ranch subpopulation's range, yet the southwest had a significantly lower reproductive rate (0.57 versus 0.80). These two subpopulations also had similar environmental and social covariate values, but southeast Manyara Ranch had a higher local adult female giraffe population density. Thus, the use of social associations to define subpopulations elucidated a new level of biologically meaningful population structure.

Here we offer evidence that the trade-off by adult females between aggregating in higher densities and maintaining strong relationships with more community members, versus lowering predation risk to calves by roaming closer to human settlements had positive demographic results, with higher reproductive rates near towns and bomas despite lower social cohesion in those areas. Previous research in this metapopulation found that in giraffe social communities closer to bomas, adult females had weaker and more exclusive relationships with other community members (Bond, König, Lee, Ozgul, & Farine, in revision). We posited that the

presence of humans on foot disrupted social cohesion and forced giraffes to form smaller groups. At the same time, however, giraffe groups with calves were more likely to be found closer to bomas, likely because of reduced predator densities there (Bond, Lee, Ozgul, & König, 2019). Areas with more dense bushlands tended to be farther from towns, and also supported lower densities of adult female giraffes—conditions that were associated with lower calf survival. Meanwhile adult female relationship strength and social exclusivity had no influence on demographic rates among subpopulations. We stress, however, that giraffes do not roam close to towns in general, as the closest observation of a giraffe group to a town was 0.35 km, and the next-closest group was 1.01 km. In comparison, the closest giraffe group to a boma was 0.02 km, and 289 groups were within 1.01 km of a boma. Thus, some general proximity to towns likely reduces natural predation on calves but overall giraffes still maintain their distance from large, densely populated human settlements compared to bomas.

Spatial structure of populations is a central concern to biologists (Thomas & Kunin, 1999), but the application of objective, biologically meaningful clustering techniques to define populations for demographic analysis has been rare. Our approach adds to the few techniques available to ecologists to define continuous populations to better understand the spatial versus social drivers of population dynamics. Earlier work on this problem by Coulson, Albon, Pilkington, & Clutton-Brock (1999) used data on the distances between every pair of Soay sheep (*Ovis aries*) and hierarchical cluster analysis to define groups. Schaefer et al. (2001) used fuzzy cluster analysis of radio-telemetry locations to group woodland caribou (*Rangifer tarandus caribou*). Ball, Finnegan, Manseau, & Wilson (2010) combined telemetry location data with genetic data and individual-based clustering to delineate spatial structure for woodland caribou. We support the notion that the foundation for defining population and subpopulation structures

should be the patterns of affiliation among individuals (Harwood, 2009; Nagy et al., 2011). Social groups also share many similarities in environmental factors that affect fitness, i.e. food and water resources, predation pressure, and cover, so within-group variation in survival and reproductive rates should be less than variation among groups. Indeed, we documented demographic differences among socially defined subpopulations, with subpopulation dynamics being driven by common endogenous or environmental variables but also to some extent the local giraffe population density.

Further work is needed to examine whether variation in fitness traits among subpopulations is influenced more by some inherent aspect of the phenotypes in a social community (Farine, Motiglio, & Spiegel, 2015), rather than spatially explicit factors such as vegetation or anthropogenic pressures or population density. Fine-scaled mapping of vegetation quality rather than type may also provide a better understanding of why adult female giraffes congregate in higher densities in certain areas, which was correlated with higher calf survival.

Overall, we believe social relationships among individuals are a biologically meaningful basis for defining population structure, and should be used where possible to better understand demographic variation within a larger population. Tools for using association-based delineations of subpopulations are now widely available thanks to advancements in the field of social network analysis (Croft, James, & Krause, 2008; Wey, Blumstein, Shen, & Jordan, 2008; Whitehead, 2008). There may be practical limitations given the expense of collecting comprehensive social network data, and the difficulty of sampling a large population over a large area, but technological advances such as automated tracking and pattern recognition are permitting ever-larger sample sizes in continuous populations with individually identified animals. Despite

sampling limitations, these techniques yield new insights into variation in population and demographic structure.

CONCLUSIONS

Masai giraffes were recently categorized as endangered on the IUCN Red List (Bolger et al., 2019) so targeted conservation actions to improve population growth rates in increasingly human-dominated landscapes are needed to help reverse extinction risk. Conservation and adaptive management of wildlife in the 21st century involves identifying appropriate evolutionarily significant units and management units that are relevant for understanding population dynamics, and characterizing trends within those units before and after applying management actions (Ryder, 1986; Moritz, 1994). These units should comprise individuals that are likely to share the same space at the same time, thus be exposed to the same environmental characteristics and face the same social constraints (Conradt, Clutton-Brock, & Guinness, 1999; Coulson, Albon, Pilkington, & Clutton-Brock, 1999). This also enables more targeted and effective conservation measures to be developed for at-risk species (Sommer & Ozgul, 2019). Population biologists and managers would benefit from additional tractable tools to delineate and explore fine-scale population structure and demographic variation in biologically meaningful ways, and social network analysis provides that tool.

Supplementary Materials

STUDY AREA

The Tarangire Ecosystem of northern Tanzania supports one of the most diverse large-mammal communities in the world (Lamprey, 1964). It is situated in the eastern branch of the Great Rift Valley and encompasses roughly 30,000 km^2 (Prins, 1987). The TE experiences three

precipitation seasons per year (short rains = Oct–Jan, long rains = Feb–May, and dry = Jun–Sep), and average monthly precipitation by season were short rains = 63 mm, long rains = 100 mm, dry = 1 mm (Foley & Faust, 2010).

Land management is divided among Tarangire National Park, Lake Manyara National Park, Manyara Ranch Conservancy, and Mtowambu and Lolkisale Game Controlled Areas. The two national parks, Tarangire and Lake Manyara, have high levels of wildlife protection including exclusion of livestock and human settlements and rigorous anti-poaching patrols; Manyara Ranch has intermediate levels of wildlife protection with no human settlements and some anti-poaching patrols but with large numbers of livestock and herders present during the daytime. Lolkisale has permanent human settlements, many livestock, sport hunting areas, and a village Wildlife Management Area with similar levels of anti-poaching efforts as Manyara Ranch; and Mtowambu has human settlements, many livestock, and sport hunting, but no Wildlife Management Area. All administrative areas are connected by movements of adult females (Lee & Bolger, 2017). Agriculture in the TE outside of the protected areas increased fivefold from 1984 to 2000 causing substantial habitat loss, increasing fragmentation, and reducing connectivity (Msoffe et al., 2011).

The Rift Valley escarpment, a steep cliff that restricts giraffe movements, forms the western boundary of the study area. West of Tarangire National Park, south of Lake Manyara National Park, and east of Makuyuni town, wild large mammals are rarely observed due to high human and livestock population density and agriculture. Two 2-lane asphalt roads cross the study area.

FIELD DATA COLLECTION

We surveyed following a robust design (Pollack, 1982), with three primary sampling periods per year near the end of each precipitation season (Jan, May, and Sep). Each primary sampling period was composed of two independent, back-to-back secondary sampling periods during which we drove all transects one time. Each primary sampling period took approximately 20–30 days (10–15 days per secondary period). Transect density throughout the study area was high (0.42 km/km^2) relative to average adult female giraffe home range (115 km^2; Knüsel, Lee, König, & Bond, 2019). Driving speed was maintained between 15 and 20 km/h on all transects, and all survey teams included the same two observers and a driver.

During surveys, we encountered a sample of individuals that we 'captured' or 'recaptured' by photographing their coat patterns. We recorded the following data for each individual: age class (calf, subadult, adult), sex (male, female), and GPS location of the group formation (unique set of individuals observed together on a given survey). We used a suite of physical characteristics, including body shape, relative length of the neck and legs, ossicone characteristics, and height to categorize giraffes into the three age classes: calf (<1 year), subadult (1–3 years), or adult (>3 years).

CREATING THE DATASET

To identify individuals we utilized Wild-ID (Bolger, Morrison, Vance, Lee, & Farid, 2012), a computer program that matches unique patterns from photographs. We included data from the 2011 pilot survey to create the social network and estimate reproductive rates, but excluded these observations from encounter histories for survival analysis because we did not conduct the dry season survey after the pilot survey in the long rains. We began with a total population of 1,139 adult and older subadult females in our dataset; older subadults were those classified as adults at some point during our 6-year study period. We used these individuals to

calculate local adult female giraffe population densities. We also began with a total population of 916 calves. For our network and survival analyses, we selected only females that were adults during the first full year of our study (N = 891 adult females). This dataset included most of the adult females in the study area, as 80% had been identified by the end of the first year of the study (Bond, König, Lee, Ozgul, & Farine, in revision). To maximize the accuracy of the network we used only adult females seen > 5 times (Davis, Crofoot, & Farine, 2018), resulting in a subsample of 540 females to assign subpopulation (community) membership. We then assigned each adult female with $\leq$ 5 detections, and each calf, to a subpopulation based on their presence in group formations with the adult females who were used in the network. For each unique group formation, we counted the frequency of subpopulation assignments of females from the network. We then attributed the calves and lower-detection adult females in that unique group to the subpopulation with the highest frequency, combined all the subpopulation assignments for each individual, and assigned it to the majority subpopulation. We omitted adult females and calves seen at equal frequencies in more than one subpopulation, as well as calves that were always seen with females without a subpopulation assignment or not seen with any females. This process yielded a subsample of 772 adult females and 807 calves. We further subsampled the dataset by removing individuals from four subpopulations with too few adult females or calves to estimate survival ($N \leq 25$). For the survival analysis we also discarded 12 adult females and 12 calves detected only during the 2011 pilot survey and never seen again. The final dataset contained encounter histories for giraffes in 10 subpopulations spanning the entire study area, including 684 adult females (mean = 68 per subpopulation, range = 27–93) and 744 calves (mean = 74 per subpopulation, range 43–133) for estimating reproductive rates, and 672 adult females (mean = 67 per subpopulation, range = 26–93) and 732 calves (mean = 73 per

subpopulation, range = 43–133) for estimating apparent survival rates. The final dataset included 75% of all known adult females and 80% of all known calves identified in our metapopulation over the 6-year study period.

ANALYSING SOCIAL NETWORKS AND DELINEATING COMMUNITIES

We created a network of adult female individuals and their social associations based on their presence together in unique group formations observed in the field. We defined a group formation as one or more giraffes that were foraging or moving together but were not moving past each other in opposite directions, and were >500 m from the next closest group formation. We used the gambit of the group to define associations, meaning individuals detected in the same group formation were considered associated at that time (Whitehead & Dufault, 1999). Our study design involved repeatedly measuring individually identified giraffes, with each individual assigned to only one group formation per primary sampling period, and with the same or a different set of individuals in groups during subsequent primary sampling periods.

In network terminology, the individuals are called ‘nodes’, and the associations among individuals are called ‘edges’. Social network analysis generates a network (association matrix) based on dyadic associations between nodes with weighted edges representing repeated associations over time. Algorithms can then partition the network into communities (other terms are demes, groups, clusters, modules, or subunits) based on denser connections (i.e. more edges) representing higher association rates within communities than among communities. This feature of real networks is called community structure (Girvan & Newman, 2002), and communities are groups of nodes which likely share common properties within the network graph. In our case, we presume giraffes within a community share common environmental influences.

Girvan and Newman (2002) proposed using an algorithm that identifies and successively removes edges lying between communities, which after some iteration leads to the isolation of the communities. A good module division provides many edges within communities and few between, and is quantified by a modularity coefficient known as *Q* (Newman, 2003). The coefficient *Q* is the sum of associations for all dyads belonging to the same community minus its expected value if dyads associated at random, given the strengths of associations among the different individuals; the 'best' clustering of a network is the division that maximizes *Q* (Newman & Girvan, 2004). The robustness of the community assignment can then be assessed using bootstrapping and the metric 'community assortativity' (r_{com}), which takes into consideration the detectability of associations (Shizuka & Farine, 2016).

We calculated the strengths of associations (i.e. edge weights) among pairs of adult female giraffes using the simple ratio index of association (Cairns & Schwager, 1987; Whitehead, 2008) which quantifies associations on a scale from 0 (two individuals never seen together) to 1 (two individuals always seen together). We conducted all analyses in R version 3.6.1 (R Core Development Team, 2019) using package *asnipe* (Farine, 2013) to create the network and calculate edge weights and edge weight coefficients of variation, package *igraph* (Csárdi & Nepusz, 2006) to graph the network and run the cluster-walktrap community-detection algorithm, and package *assortnet* (Farine, 2016) to test the robustness of the community assignments.

In a previous study (Bond, König, Lee, Ozgul, & Farine, in revision), we found that the cluster-walktrap algorithm provided the most robust community delineation from the resulting social network. The cluster-walktrap community detection algorithm parsed the adult female giraffe metapopulation into 14 distinct communities with $Q = 0.742$, demonstrating a relatively

high degree of modularity. A bootstrap test indicated the assignments of individuals to communities was robust (r_{com} = 0.749). The high Q and r_{com} values suggest strong community structure and high community fidelity with a low tendency for adult females to mix with other communities (Shizuka & Farine, 2016). Four of the communities contained too few adult females and calves to estimate survival so we limited our further analyses to the remaining 10 communities.

CALCULATING ENVIRONMENTAL COVARIATES

To generate subpopulation home ranges and calculate environmental covariates, we plotted all giraffe group locations on a GIS using ArcMap 10.8 (Environmental Systems Research Institute, Redlands, CA, USA). We used locations from all individual adult females in each subpopulation combined to generate subpopulation home ranges from 95% utilization distributions with a kernel density estimator (Seaman & Powell, 1996), using the package *adehabitatHR* in R (Calenge, 2006). We created a land cover map for the vegetation types deciduous bushlands and volcanic soil grasslands from a potential natural vegetation map developed by the University of Copenhagen's Vegetation and Climate Change in Eastern Africa project (Kindt et al., 2011). To calculate proportion of vegetation types in the subpopulation home ranges we used the function 'intersect' in package *raster* for R (Hijmans & van Etten, 2012). We mapped all towns and bomas using Google Earth (Mountain View, CA, USA) aerial imagery from June 2014. We defined towns as polygons and calculated the distances from their edges, whereas bomas were smaller features approximately 100 m across that were defined as a point in the centre of the boma. To calculate distances to bomas and towns we used the "Generate Near Table" function in the Analysis Tools toolbox in ArcMap™.

CORRELATIONS AMONG SOCIAL AND ENVIRONMENTAL COVARIATES

Spearman's rank correlation tests indicate that the covariate distance to town was negatively correlated with proportion of volcanic grasslands, and positively correlated with proportion of dense bushlands, and that local giraffe population density was negatively correlated with proportion of dense bushlands (Table S1, below). Relationship strength and social exclusivity were negatively correlated (Table S1, below). None of the other environmental covariates were significantly correlated with each other, and no environmental covariates were significantly correlated with the social covariates. No covariates were used together in the same models.

Table S1. Spearman rank correlations and p-values for environmental and social predictor variables. Bold indicates significant correlation.

Spearman correlation coefficients							
	boma	town	volc	bush	dens	ew	ewcv
boma	1						
town	0.64	1					
volc	-0.57	**-0.81**	1				
bush	0.58	**0.78**	-0.53	1			
dens	-0.39	-0.62	0.37	**-0.83**	1		
ew	0.2	-0.32	0.17	-0.11	-0.09	1	
ewcv	-0.21	0.28	-0.12	0.1	-0.02	**-0.96**	1

P-values							
	boma	town	volc	bush	dens	ew	ewcv
boma							
town	0.05						
volc	0.09	**0.00**					
bush	0.08	**0.01**	0.11				
dens	0.26	0.05	0.29	**0.00**			
ew	0.58	0.37	0.63	0.76	0.80		
ewcv	0.56	0.43	0.73	0.79	0.96	**0.00**	

Table S2. Proportion of overlap of kernel home ranges among 10 socially defined subpopulations of adult female giraffes, and number of subpopulations overlapped.

	SSE TNP/ LGCA	LMNP	Central TNP	N MR/ MGCA	NNW TNP	SW TNP	NNE TNP/ LGCA	SE MR	SW MR	W TNP
SSE TNP/LGCA	1	0	0.39	0	0.04	0.21	0.16	0	0	0
LMNP	0	1	0	0	0	0	0	0	0	0
Central TNP	0.54	0	1	0	0.27	0.29	0.22	0	0.05	0.15
N MR/MGCA	0	0	0	1	0	0	0	0.56	0.59	0
NNW TNP	0.08	0	0.39	0	1	0	0.66	0	0.43	0.13
SW TNP	0.46	0	0.45	0	0	1	0.01	0	0	0
NNE TNP/LGCA	0.25	0	0.25	0	0.53	0.01	1	0	0.35	0.01
SE MR	0	0	0	0.63	0	0	0	1	0.54	0
SW MR	0	0	0.06	0.31	0.38	0	0.39	0.25	1	0.03
W TNP	0	0	0.73	0	0.43	0	0.05	0	0.13	1
Maximum proportion overlapped by another	0.54	0	0.45	0.63	0.53	0.29	0.66	0.56	0.59	0.15
Number overlapped	4	0	6	2	5	3	6	2	6	4
Mean proportion overlapped by others	0.33	0	0.38	0.47	0.33	0.17	0.25	0.41	0.35	0.08

Table S3. Model selection results for nuisance parameters of temporary emigration, capture, and recapture probabilities for adult females and calves among 10 subpopulations of Masai giraffes in the Tarangire Ecosystem, northern Tanzania, 2012–2016.

Model	AIC_c	ΔAIC_c	AIC_c Weights	Model Likelihood	Num. Par	Deviance
Adult Female Temporary Emigration						
{S(g) γ''(dist) γ'(dist) p(g*t) c(g*t)}	19132.95	0.00	0.99	1.00	458	35129.13
{S(g) γ''(.) γ'(.) p(g*t) c(g*t)}	19143.44	10.49	0.01	0.01	456	35144.36
{S(g) γ''(g) γ'(g) p(g*t) c(g*t)}	19153.72	20.77	0.00	0.00	474	35111.89
Adult Female Capture and Recapture Probability						
{S(g) γ''(dist) γ'(dist) p(g*t) c(g*t)}	19132.95	0.00	1.00	1.00	458	35129.13
{S(g) γ''(dist) γ'(dist) p(g+t) c(g+t)}	19194.33	61.38	0.00	0.00	298	35558.11
{S(g) γ''(dist) γ'(dist) p(g) c(g)}	19964.14	831.19	0.00	0.00	34	36888.74
{S(g) γ''(dist) γ'(dist) p(t) c(t)}	20187.12	1054.17	0.00	0.00	44	37091.44
Calf Temporary Emigration						
{S(g) γ''(.) γ'(.) p(g*t) c(g*t)}	11386.97	0.00	0.92	1	462	15899.99
{S(g) γ''(dist) γ'(dist) p(g*t) c(g*t)}	11390.94	4.97	0.08	0.08	464	15899.60
{S(g) γ''(g) γ'(g) p(g*t) c(g*t)}	11426.97	40.99	0	0	480	15892.41
Calf Capture and Recapture Probability						
{S(g) γ''(g) γ'(g) p(g*t) c(g*t)}	11426.97	0.00	1	1	480	15892.41
{S(g) γ''(g) γ'(g) p(g+t) c(g+t)}	11568.29	141.32	0	0	80	16988.60
{S(g) γ''(g) γ'(g) p(t) c(t)}	11700.19	273.23	0	0	60	17162.23
{S(g) γ''(g) γ'(g) p(g) c(g)}	11784.25	357.29	0	0	49	17269.02

Table S4. Tukey's multiple comparison tests for significant differences in reproductive rate (calves to adult females) among 10 socially defined subpopulations of Masai giraffes in the Tarangire Ecosystem, northern Tanzania, 2011–2016. Numbers represent *P*-values, and bold indicates significant difference.

	SSE TNP/LGCA	LMNP	Central TNP	N MR/MGCA	NNW TNP	SW TNP	NNE TNP/LGCA	SE MR	SW MR
LMNP	1.00								
Central TNP	1.00	1.00							
N MR/MGCA	0.65	0.93	0.99						
NNW TNP	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**					
SW TNP	1.00	1.00	0.99	0.53	**< 0.001**				
NNE TNP/LGCA	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	1.00	**< 0.001**			
SE MR	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	0.98	**< 0.001**	0.95		
SW MR	**0.04**	0.16	0.34	0.91	**< 0.001**	**0.02**	**< 0.001**	**0.00**	
W TNP	0.58	0.90	0.98	1.00	**< 0.001**	0.46	**< 0.001**	**< 0.001**	0.92

Chapter 4

Sociability increases survival of adult female giraffes

Monica L. Bond · Derek E. Lee· Damien Farine · Arpat Ozgul · Barbara König

Abstract Studies increasingly show that social behaviour plays an important role in determining fitness. The extent to which social interactions between individuals drive variation in their survival in conjunction with their environment, including both the natural environment and anthropogenic influences, remains largely unexplored in wild animal societies. We examine the relative contributions of sociability (gregariousness, relationship strength, and betweenness), the natural environment (food sources and vegetation types), and anthropogenic pressures (distance from traditional pastoralist dwellings and intensely populated towns) to adult female survival in a metapopulation of Masai giraffes (*Giraffa cemelopardalis tippelskirchi*) in northern Tanzania. Using photographic capture-recapture data from 512 females over 5 years, we investigated the relative importance of social versus environmental factors in determining survival of adult females. Giraffes live in a fission-fusion society, and we found that gregariousness (average group size) and betweenness (associating with multiple groups) were more important in explaining variation in survival than natural or anthropogenic environmental factors. Relationship strength, both the average and maximum number of times two individuals were together in the same groups, was not associated with survival. We propose that giraffe societies share similarities with other 'weak tie' social systems with high fission-fusion dynamics, such as some primates, whereby survival is improved by being well-integrated into a larger community, but not by strong and stable bonds with a few individuals. Because longevity is the most important determinant of a female giraffe's lifetime reproductive success (LRS),

flexible bonds with many other females may allow individuals to overcome adverse and unpredictable environmental conditions to increase their survival and thus their fitness.

Keywords social network analysis, survival, fitness, giraffe, *Giraffa camelopardalis*, fission-fusion society

Introduction

The combination of the social and physical environment comprises the socio-ecological landscape in which natural selection takes place (Webber and Vander Wal 2017). Within this landscape, sociality will evolve if a social trait increases an individual's fitness through higher reproductive success or survival (Alexander 1974, Silk 2007, Clutton-Brock 2016). By combining social and demographic information we can determine the fitness consequences of sociability, and thus identify selection pressures that might shape social behaviour (e.g., Lusseau and Newman 2004, Silk et al. 2009; 2010, Frère et al. 2010, Barocas et al. 2011, Stanton and Mann 2012, McFarland et al. 2017, Alberts 2019). In addition to social environment, an individual's physical environment also mediates their reproductive success and survival. Further, social interactions can be dependent on the physical environment and the effects of the physical environment can be mediated through social interactions. The relative influences of social versus physical environmental factors, as well as their interactions, on fitness and animal population dynamics remain largely unexplored.

Many animal species exhibit a gradient of sociality, for example in fission-fusion societies where groups of associates merge and split at varying frequencies (Kummer 1971, Aureli et al. 2008). These dynamics can lead to complex, multi-level social structure with closely bonded associates living within larger social communities of more loosely connected individuals, and variable group sizes (VanderWaal et al. 2014, Papageorgiou et al. 2019, Bond et al. in press).

Variable social environments often characterize species living in heterogeneous ecological environments that might favour the evolution of multiple social phenotypes stemming from the same genotype (Taborsky and Oliveira 2012, Schradin et al. 2012). Indeed, population density and resource predictability can impact whether individuals of the same species and even the same individuals are found living either a solitary or gregarious lifestyle, termed social flexibility (Schradin et al. 2012). An individual's tendencies toward higher or lower sociability depending on the socio-ecological landscape are assumed to result in improved survival and reproductive success.

Network analysis (Whitehead 2008) has been widely used to investigate how sociability connects with fitness. Baboons (*Papio cynocephalus*; Silk et al. 2010) and rhesus macaques (*Macaca mulatta*; Ellis et al. 2019) that form strong, stable social bonds live longer, and centrality within social networks—the measure of an individual's structural importance in a group based on its network position—is correlated with survival in rock hyraxes (*Procavia capensis*; Barocas et al. 2011), bottlenose dolphins (*Tursiops* sp. Stanton and Mann 2012), and bighorn sheep (*Ovis canadensis*; Vander Wal et al. 2015). Rhesus macaques (Ellis et al. 2019) that spend the most time interacting with many others in their networks have higher survival probabilities, and more socially integrated feral horses (*Equus ferus*) have greater reproductive success (Cameron et al. 2009). Natal dispersal of female yellow-bellied marmots (*Marmota flaviventrus*) was less likely for individuals that had more frequent friendly interactions with mothers and played more frequently with others (Armitage et al. 2011). These demographic studies of sociality did not incorporate the influence of the physical environment on survival and/or reproduction. Combining social, ecological, and demographic data provides an

opportunity to investigate what component(s) of an animal's socio-ecological environment is most important to their survival.

Here we explore how variation in both the ecological and social environment affect adult female survival in a metapopulation of giraffes (*Giraffa camelopardalis tippelskirchi*) living in a fission-fusion social system. Giraffes are long-lived, non-migratory, browsing ungulates (Dagg 2014). Age of first reproduction for female giraffes in the wild is approximately 5-6 yr (Bercovitch and Berry 2009); females can have a twenty-year breeding tenure, and lifespan accounts for the majority of variance in lifetime reproductive success (Bercovitch and Berry 2016). The primary natural predators of giraffes are lions (*Panthera leo*), although lions rarely prey upon adults (Strauss and Packer 2013). Among giraffes, adult female survival contributes the most to spatial variation in population growth rates (Lee et al. 2016a). Adult female giraffes have stronger preferences in their social associations (Carter et al. 2013a) and form longer-term associations with other females than do adult males and maturing, dispersing subadults (Bercovitch and Berry 2012, Carter et al. 2013b). Adult female survival in our study area was lower outside protected areas than inside, possibly due to poaching and/or habitat loss (Lee et al. 2016a). Furthermore, relationship strength and exclusivity – preferentially associating with fewer individuals – within adult female social communities was affected by proximity to traditional human settlements (Bond et al. in press). Given increasing evidence that social behaviour plays an important role in determining fitness, yet survivorship is also influenced by ecological factors, our aim was to document the relative importance of individual sociability versus that of the physical environment in affecting survival of adult females. If an adult female giraffe's sociability increases her survival, this is likely to increase her lifetime reproductive success.

Here, we quantify measures of social connectedness (hereafter sociability) as well as physical environmental features and consequent survival probabilities using mark-recapture data from 512 individually identified adult female giraffes in the Tarangire Ecosystem (Fig. 1) over a 5-year period. We indexed sociability by four metrics derived from social network analysis: the strength of relationships (mean and maximum), gregariousness (average group size), and the extent to which an individual links to other adult females that are not directly connected (betweeness). We then model how these social traits explain variation in survival rates relative to the variation in survival arising from individuals' physical environment, including vegetation types, prevalence of preferred forage plants, and distance from low- and high-impact human settlements. We consider two scales of social and physical environmental variables that might influence survival: at the level of the social community and the level of the individual. We test ten specific predictions (see methods) in order to evaluate the relative importance of sociability compared to physical environmental factors in determining survival among giraffes living in multi-level communities characterized by fission-fusion dynamics.

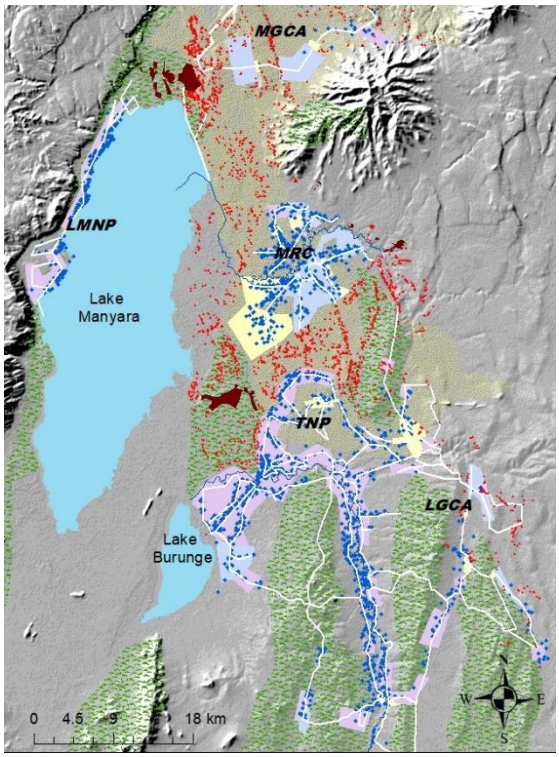

Figure 1. Locations (blue diamonds) of groups of adult female giraffes and environmental covariates in the Tarangire Ecosystem of northern Tanzania, 2011–2016. LMNP is Lake Manyara National Park, TNP is Tarangire National Park, MRC is Manyara Ranch Conservancy, MGCA is Mtowambu Game Controlled Area, and LCGA is Lolkisale Game Controlled Area. White lines are dirt tracks surveyed for giraffe groups, blue lines are rivers, red points are bomas, and maroon polygons are towns. Yellow dots are grasslands on volcanic soils, and green stippling is dense bushlands. Pale yellow polygons are stands dominated by >10% *Dichrostachys cinerea*, pale blue by *Acacia drepanolobium*, and lavender by *Acacia tortilis*.

Methods

STUDY AREA

We selected the Tarangire Ecosystem in northern Tanzania as our study area because it is a heterogeneous landscape with varying degrees of anthropogenic pressures on wildlife, ranging from habitats deep within protected national parks to those in close proximity to towns and traditional homesteads of indigenous people, called bomas (Fig 2a-b). Bomas are dispersed family compounds of several huts constructed with natural materials, and towns consist of dense concentrations of concrete structures. Bomas in our study area are occupied by indigenous pastoralist Masai people who typically do not poach giraffes for meat, but may kill lions and other carnivores to protect livestock (Kissui 2008). Towns are much rarer, but also much more densely populated by people, typically surrounded by farmlands, and inhabited by bushmeat poachers who often target giraffes (Kiffner et al. 2015).

The Tarangire Ecosystem is a savanna biome with variation in vegetation types ranging from open grasslands to dense deciduous bushlands and thickets (Lamprey 1963), supporting one of the most diverse large-mammal communities in the world (Lamprey 1964). Our study area in the core of the Tarangire Ecosystem is 4400 km^2 where we sampled a 1500 km^2 area along road transects in five administrative areas with differing management activities (Fig. 1). Land management is partitioned among Tarangire National Park (TNP), Lake Manyara National Park (LMNP), Manyara Ranch Conservancy (MRC), and Mtowambu (MGCA) and Lolkisale Game Controlled Areas (LGCA). The two national parks, TNP and LMNP, have high levels of wildlife protection including exclusion of livestock and human settlements and rigorous anti-poaching patrols; MRC has intermediate levels of wildlife protection with exclusion of human settlements and some anti-poaching patrols but with large numbers of livestock during the daytime. The

northern portion of LGCA incorporates a new (since 2014) village Wildlife Management Area with similar levels of anti-poaching efforts as MRC but with sport hunting and permanent human settlements permitted, and MGCA and the southern portion of LCGA have extensive sport hunting and permanent human settlements. All administrative areas are connected by movements of adult female giraffes (Lee and Bolger 2017).

The Rift Valley escarpment, a steep cliff that restricts giraffe movements, forms the western boundary of the study area. Wild large mammals are rarely observed east of Makuyuni town along the asphalt road due to high human and livestock population densities, or southwest of TNP and south of LMNP due to widespread intensive agriculture. Two 2-lane asphalt roads cross the study area (Fig. 1).

DATA COLLECTION

We used photographic capture-mark-recapture techniques to identify individual giraffes from the coat markings unique to each animal (Foster 1966). We utilized the computer program Wild-ID to match patterns from photographs: this program performs with little misidentification error in large giraffe datasets (Bolger et al. 2012).

We conducted 30 independent, daytime, fixed-route road-transect surveys to photograph giraffes between January 2012 and October 2016. The Tarangire Ecosystem experiences three precipitation seasons per year (short rains = Oct–Jan with an average monthly precipitation of 63 mm; long rains = Feb–May with 100 mm/mo; and dry = Jun–Sep with 1 mm/mo; Foley and Faust 2010). We surveyed for giraffes near the end of each season according to a robust design with a primary sampling period composed of two independent, back-to-back secondary sampling periods during which we drove all transects in the study area (Pollack 1982). All survey roads were dirt tracks. Road density throughout the study area was high (0.42 km/km^2) relative to

giraffe home-range size (115 km^2; Knüsel et al. 2019). We maintained driving speed between 15 and 20 kph on all transects, and all survey teams included the same two dedicated observers and a driver. We sampled each road segment only one time in a given event, and each primary sampling period took approximately 21–30 days.

When we encountered giraffes, we 'marked' or 'resighted' individuals by driving to within 150 m distance and photographing them. We recorded the following data: age class (calf, subadult, adult), sex (male, female), and GPS location. We used a suite of physical characteristics, including body shape, relative length of the neck and legs, ossicone characteristics, and height to categorize giraffe into sex and age classes. Wild giraffes can experience first estrous at 4 years of age (Bercovitch and Berry 2009), thus we considered these as adults. In our dataset we considered only females first observed during the initial year of the study and who were adults the first time they were observed. We used the gambit of the group—individuals present together in the same group formation—to define associations (Whitehead and Dufault 1999). We defined a group formation as one or more giraffes that were foraging or moving together, and with >500 m between the closest member of another group (Carter et al. 2013a;b, VanderWaal et al. 2014, Bond et al. 2019). Our study design involved repeatedly measuring individually identified giraffes, with each individual assigned to only one group formation per primary sampling period, but with the same or a different set of individuals in groups during other primary sampling periods.

DATA ANALYSIS

Social covariates—We created a matrix of individual adult females and their associations to generate a social network and calculate a set of metrics representing attributes of each female's social tendencies. In network terminology, the individuals are called 'nodes', and the

associations among individuals are called ‘edges’. Weighing edges takes into account the number of times a pair of nodes (dyad) was seen together. To calculate edge weights between individual giraffes, we applied the simple ratio index of association (Cairns and Schwager 1987, Whitehead 2008; see Supplementary Materials for equation) which quantifies associations on a scale from 0 (two individuals never seen together) to 1 (two individuals always seen together). Higher edge weights represent more times a pair of giraffes were seen in the same group formations over the study period, hence a stronger relationship between them.

We calculated four measures of individual giraffe sociability, assuming higher values of each translate to greater sociability. We calculated the strength of each female’s relationships with three measures (see Supplementary Materials Fig. S1 for histograms of the count values): (1) her mean non-zero edge weight, calculated as the sum of her edge weights divided by her total number of associates (also called ‘weighted degree’); (2) her maximum edge weight with any of her associates; and (3) the coefficient of variation of her edge weights. We calculated each female’s (4) gregariousness score as the count of the number of adjacent edges, which is equivalent to her average group size minus one (known also as ‘degree’). This metric represents her tendency to be in larger or smaller groups. Lastly, we quantified each female’s (5) betweenness score, which is a count of the number of shortest paths between other nodes that flow through the node representing that individual (Butts 2016). Betweenness measures how important that female is for connecting disparate parts of the network: individuals with high betweenness scores are more likely to link independent groups or communities and may tend to change groups more often than others.

Social network analysis can be used to partition populations into social communities (also known as modules) based on denser connections (i.e. more edges) representing higher

association rates within than among communities (Newman 2003; 2006). We assigned our subsample of adult female giraffes to social communities and tested whether grouping these females together in our survival analysis improved model fit, because we assumed individuals within the same communities would be subject to similar social and physical environmental influences. See Bond et al. (in press) and Supplementary Materials for community detection methods.

Our full dataset includes life histories for 1139 individually identified adult females observed in 2137 different group formations over the 5-year study period. We subsampled the adult females to those with at least six observations to improve the accuracy of the edge weights (Davis et al. 2018). However, to calculate gregariousness for our subsample we generated a separate network using all adult females regardless of their number of observations, so that the resultant gregariousness score for the subsample incorporated actual group sizes. Community detection of the subsample parsed the adult female metapopulation into 14 distinct social communities, but we excluded members of four communities that contained <15 individuals. The remaining 10 communities contained an average of 51 individuals each (range = 28–70) and a total of 512 adult females, which became our final dataset for modelling seasonal apparent survival probabilities.

We constructed networks and conducted analyses in R version 3.6.1 (R Core Development Team 2019) using the package *asnipe* (Farine 2013) to create the association matrix and calculate edge weights; the package *sna* (Butts 2016) to calculate betweeness; and the package *igraph* (Csárdi and Nepusz 2006) to calculate each individual's degree (gregariousness) and run the community detection algorithm.

Physical environmental covariates— We plotted locations of giraffe group formations on a GIS using ArcMap 10.8 (Environmental Systems Research Institute, Redlands, CA, USA), and extracted at every location natural and anthropogenic environmental variables of vegetation and proximity to nearest human settlements of towns and bomas (Fig. 1). We used a combination of publicly available remote-sensed data and our own ground-based vegetation surveys to create GIS vegetation features. We mapped two broad vegetation types (Fig. 2c-d): (1) deciduous bushland and thicket and (2) edaphic grassland on volcanic soils with scattered woody species (Kindt et al. 2011), derived from a natural vegetation map developed by the University of Copenhagen's Vegetation and Climate Change in Eastern Africa (VECEA) project. We then used ground-based observations that we collected in January 2014 every 2 km along our roads to map polygons of vegetation with >10% cover of one of three primary giraffe forage species: (1) *Acacia tortilis*; (2) *A. drepanolobium*; and (3) *Dichrostachys cinerea* (Foster 1966, Pellew 1984, Young and Isbell 1991, Furstenburg and van Hoven 1994, Caister et al. 2003). We used Google Earth (Mountain View, CA, USA) aerial imagery from June 2014 to map bomas as points and towns as polygons. To calculate distances to bomas we used the Point Distance proximity function and to calculate distances to towns we used the Near proximity function in ArcMap. For community-level environmental covariates, we calculated the 95% kernel home ranges using locations from all individuals in each community using the package *adehabitatHR* in R (Calenge 2006). We then quantified the proportion of vegetation types in the home range with package *raster* for R (Hijmans and van Etten, 2012), and average distances from the center of the community home range to the nearest boma or town in ArcMap.

Figure 2. Two types of human settlements: (a) Masai boma and (b) town. Masai giraffes in two vegetation types in the Tarangire Ecosystem: (c) deciduous bushland and thicket and (d) edaphic grassland on volcanic soils with scattered woody species.

Survival rates—We estimated apparent survival probabilities and tested hypotheses using capture-recapture methods (Lebreton et al. 1992) from individual adult female encounter histories analysed in program MARK 8.2 (White and Burnham 1999). We utilized the Pradel robust design model to provide estimates of seasonal apparent survival (*S*), temporary emigration (γ'' and γ'), and capture and recapture probabilities (*p* and *c*) (Pradel 1996, Nichols et al. 2000) and ranked models using Akaike's Information Criterion corrected for small samples (AIC_c). We were unable to conduct surveys in LMNP during the last two primary sampling periods in 2016 due to logistical constraints, so we set *p* and *c* to zero for the LMNP community for those periods. We tested a survival model that grouped females from the same social community, because we suspected these females were likely to share common influences and thus there might be potential dependencies among those individuals. To assess support for community (group) effects in *S*, *p*, and *c*, we considered community-specific parameters (g), as well as constant, equal parameter values for all communities, denoted (.) We always included group effects in immigration (γ') and emigration (γ"). We ranked models to find the most parsimonious structure, beginning with the most fully parameterized model in our set with constraints (group effects) on the parameter of interest (*S*), but with both group and temporal effects (g * t) in capture and recapture rates. Temporal effects means that capture and recapture rates vary by survey. We also considered that larger group sizes might increase detectability, so we modelled gregariousness as a covariate to *p* and *c* (g * t + gregariousness). We ranked all possible combinations of models of group and constant effects. After selecting the best model of group and constant effects, we added the effects of social and physical environmental covariates on apparent survival. All individual covariates were standardized. We also modelled local giraffe population density as a covariate, as this is known to influence adult female survival probabilities

for some other ungulates (Vander Wal et al. 2015 but see Bonenfant et al. 2009). Local giraffe population density includes all adult female giraffes ever detected within the home range of the social community, regardless of number of detections or community assignments (N=1139 adult females).

Throughout model ranking and selection, we used the logit link function and 2nd part estimation (Cooch and White 2019). We considered model AIC_c weights as a metric for the strength of evidence supporting a given model as the best description of the data, and parameter estimates whose 95% confidence intervals did not overlap zero as significant effects (Burnham and Anderson 2002). There is no goodness-of-fit test of whether the most general Pradel model in our candidate model set adequately fits the data for robust design (Cooch and White 2019). Therefore, to test goodness-of-fit, we combined our secondary samples to a simple binary variable (seen, not seen), and treated the resulting encounter history as a live encounters Cormack-Jolly-Seber (CJS) model (Cooch and White 2019). We then tested the fit of our data to the fully time-dependent CJS model using Program RELEASE TEST 2 + TEST 3 (Burnham et al. 1987), and median ĉ (Cooch and White 2019).

Testing effects of sociability versus environment on survival—We modelled the effects of the following social and physical environmental covariates on the demographic response adult female survival. (1) average relationship strength [MEANEW]; (2) maximum relationship strength [MAXEW]; (3) coefficient of variation in relationship strengths [EWCV]; (4) gregariousness [GREG]; (5) betweenness [BETW]; (6) average distance (km) from nearest town (at the individual and community level) [TOWN]; (7) average distance (km) from nearest boma (individual and community level) [BOMA]; (8) proportion of time spent in one of two different broad vegetation types, volcanic soil grasslands [VOLC] and dense bushlands (individual and

community level) [BUSH]; (9) proportion of time spent in stands dominated by one of three preferred giraffe forage species (individual and community level), *Acacia tortilis* [ATORT], *A. drepanolobium* [ADREP], and *Dichrostachys cinerea* [DICHRO]; and (10) local giraffe population density (community level) [DENS]. We examined multicollinearity among covariates by calculating the Spearman correlation coefficient, but each model contained only one covariate.

All predictions pertain to both individual- and community-level effects. We predicted higher adult female survival (1) with increasing average and maximum relationship strength, (2) with increasing gregariousness, and (3) with increasing betweenness. Closer bonds could increase the predictability of behaviour of associates, which may reduce agonistic interactions and thus reduce stress (Bercovitch 1991). More socially isolated individuals may miss out on important knowledge about food resources and predators (Williams et al. 2017, Stutz et al. 2018) and thus have lower survival than individuals that wander in larger groups. More-mobile individuals with higher betweenness in a fission-fusion system might be able to better exploit dynamic and dispersed food resources (Maryanski 1987). Alternatively, movements among groups of less-familiar individuals might prove stressful or risky, so higher betweenness might also reduce survival. We also predicted (4) that females with stronger bonds to fewer other associates would have lower survival, as higher edge weight CVs are a signature of disrupted social systems (Maldonado-Chapparo et al. 2018).

With respect to the physical environment, we expected (5) adult female survival would decrease closer to areas of intensive human influences (towns) where habitat loss and poaching are more prevalent (Lee et al. 2016a). (6) Survival might be unaffected by distance to bomas where human influences are less intensive and where female giraffes with calves tended to

congregate, potentially due to reduced predator densities, as demonstrated in previous research in this study area (Bond et al. 2019). However, network analysis of this population also found proximity to bomas resulted in more exclusive social associations and overall weaker relationship strengths among members of adult female social communities (Bond et al. in press), so survival might decrease near bomas as a result of disruption to social structure. We expected (7) higher survival with increasing proportion of locations in grasslands on volcanic soils because volcanic soils are especially fertile, which may enhance forage quality (Hansen et al. 1985) and (8) with increasing proportion of locations in dense woodlands and thickets, which were selected by groups with calves (Bond et al 2019). We also predicted (9) higher survival with increasing proportions of locations in *A. tortilis*, *A. drepanolobium*, and *D. cinerea*, as these forage species were seasonally selected by single adult female giraffes, and female groups with calves (Pellew 1984, Young and Isabel 1991, Mramba et al. 2017, Bond et al. 2019). Finally, we expected (10) adult female survival would increase with increasing local adult female giraffe population density within the community home range (Vander Wal et al. 2015) as we presume individuals would congregate and fare better in higher-quality habitats and reproductive rates were higher in social communities with higher densities (Bond et al. in review). On the other hand, more individuals might lead to more food competition, depending on resource distribution and availability, so higher population densities might also reduce survival, although density-dependent decreases in adult female survival in ungulates tends to affect only the oldest females (Bonenfant et al. 2009).

Results

We detected no strong correlations between social and physical environmental covariates (Spearman correlation coefficients < 0.50), although several correlations between environmental

covariates were significant ($P < 0.05$); Supplementary Materials Table S1. We found no evidence for lack-of-fit in the encounter history data (TEST 2 + TEST 3 $\chi^2 = 61.844$, d.f. = 60, $P = 0.41$; median-ĉ = 1.186), therefore we kept ĉ = 1.0 for model selection (Cooch and White 2019). Our ranking of group and constant effects found constant survival across social communities, group-specific temporary emigration, and group and time interaction effects as well as gregariousness effect on *p* and *c* was the best model {S(.) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)} (Table 1). Therefore, our survival model accounted for variation in detectability due to gregariousness. Covariate models of survival with betweenness, gregariousness, and proportion of locations in *Acacia drepanlobium* were the top-ranking models and had comparable model weights (< 2 ΔAIC_c). The top model, which carried 31% of the weight in the candidate model set (Table 1), indicated adult female survival probability increased with increasing betweenness ($ß_{BETW} = 14.16$, SE = 11.72) but the 95% confidence interval for the parameter estimate overlapped zero, suggesting no statistical significance of this effect (Table 2). Females with fewer than approximately 700 shortest paths flowing through them began to exhibit lower survival rates; above that number survival probabilities showed an asymptote (Fig. 2a). The second-ranked model in the candidate set indicated that more gregarious females (i.e. with larger mean group sizes) had higher survival probabilities ($ß_{GREG} = 1.61$, SE = 0.68), and the parameter estimate for this effect was statistically significant (95% confidence interval = 0.29 – 2.94; Table 2). This second-ranked model carried 20% of the weight (Table 1). Female survival probability increased up to the point where mean group size included approximately three or more other females, and then increases in survival rate flattened (Fig. 2b). The final competitive model in the candidate set suggested that females with more locations in *A. drepanolobium* had lower survival probabilities ($ß_{ADREP} = -1.07$, SE = 1.09) but the effect was not significant as the

95% confidence interval for the parameter estimate overlapped zero (Table 2) and this model carried only 14% of weight (Table 1). Overall, individual-based covariate models were superior to group-based (community) covariate models.

Table 1. Model selection results for constant survival, group effects, and social and physical environmental covariate models of apparent adult female survival probabilities among 10 communities of Masai giraffes in the Tarangire Ecosystem, northern Tanzania, 2012–2016 (N = 512 females). Bold are competive top models (<2 ΔAIC_c).

Model[a]	AIC_c	ΔAIC_c	AIC_c Weights	Model Likelihood	Num. Par	Deviance
{S(BETW) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17277.89	0.000	0.309	1.000	468	16255.69
{S(GREG) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17278.79	0.906	0.197	0.636	468	16256.60
{S(ADREP) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17279.52	1.635	0.137	0.442	468	16257.33
{S(EW) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17281.60	3.712	0.048	0.156	468	16259.41
{S(.) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17281.81	3.919	0.044	0.141	467	16262.00
{S(VOLC) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17282.33	4.447	0.033	0.108	468	16260.14
{S(.[gTOWN]) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17282.46	4.575	0.031	0.102	468	16260.27
{S(BUSH) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17282.91	5.026	0.025	0.081	468	16260.72
{S(BOMA) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17283.16	5.276	0.022	0.072	468	16260.97
{S(.[gVOLC]) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17283.43	5.546	0.019	0.063	468	16261.24
{S(TOWN) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17283.50	5.616	0.019	0.060	468	16261.31
{S(.[gBUSH]) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17283.63	5.742	0.018	0.057	468	16261.44
{S(.[gEWCV]) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17283.79	5.899	0.016	0.052	468	16261.59
{S(.[gEW]) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17283.85	5.967	0.016	0.051	468	16261.66
{S(DICHRO) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17284.02	6.136	0.014	0.047	468	16261.83
{S(ATORT) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17284.08	6.193	0.014	0.045	468	16261.89
{S(.[gBOMA]) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17284.13	6.241	0.014	0.044	468	16261.94
{S(.[gDENS]) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17284.17	6.285	0.013	0.043	468	16261.98
{S(MAXEW) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17284.53	6.638	0.011	0.036	468	16262.33
{S(g) γ''(g) γ'(g) p(g*t+GREG) c(g*t+GREG)}}	17303.05	25.164	0.000	0.000	476	16261.75
{S(.) γ''(g) γ'(g) p(g*t) c(g*t)}}	17335.52	57.634	0.000	0.000	465	16320.48

[a] g=social community; ADREP=*Acacia drepanolobium*; ATORT=*Acacia tortilis*; BETW=betweenness; BOMA=distance (km) to nearest boma; BUSH=deciduous bushlands and thickets; DENS=local adult female giraffe population density; DICHRO=*Dichrostachys cinerea*; EW=mean edge weight; EWCV=edge weight coefficient of variation; GREG=gregariousness (degree); MAXEW=maximum edge weight; TOWN=distance (km) to nearest town; VOLC=volcanic soil grasslands.

Table 2. Parameter estimates for social and environmental covariates in competing models (<2 ΔAIC_c) for 512 adult female giraffe survival probabilities. Significant effect (95% CI does not overlap zero) in bold.

Covariate	Estimate	SE	95% lower	95% upper
Betweenness	14.160	11.710	-8.791	37.110
Gregariousness	**1.613**	**0.677**	**0.287**	**2.940**
Proportion *Acacia drepanolobium*	-1.074	1.094	-3.219	1.071

Discussion

Giraffe societies show a relatively high degree of fission-fusion dynamics, and our study revealed that adult females exhibit substantial individual variation in social behaviours, with females moving more or less frequently among group formations and spending time with more or fewer other females. Our 5-year demographic analysis of more than 500 individually identified females demonstrated that those who roamed in groups with at least three other females, and associated more often with different groups, increased their survival probabilities. Typical average group size—known as gregariousness—was a significant social effect and far more important in explaining variation in survival than any of the physical natural or anthropogenic environmental factors we tested, including factors previously shown to influence demographic rates in this population (e.g., Lee et al. 2016a, Lee and Bolger 2017, Bond et al. in review). Female flexibility in establishing and maintaining a limited number of social bonds with others living in the same larger community provides a foundation for increasing their survivorship. Adult female social phenotypes exhibiting greater sociability had the highest survival probabilities.

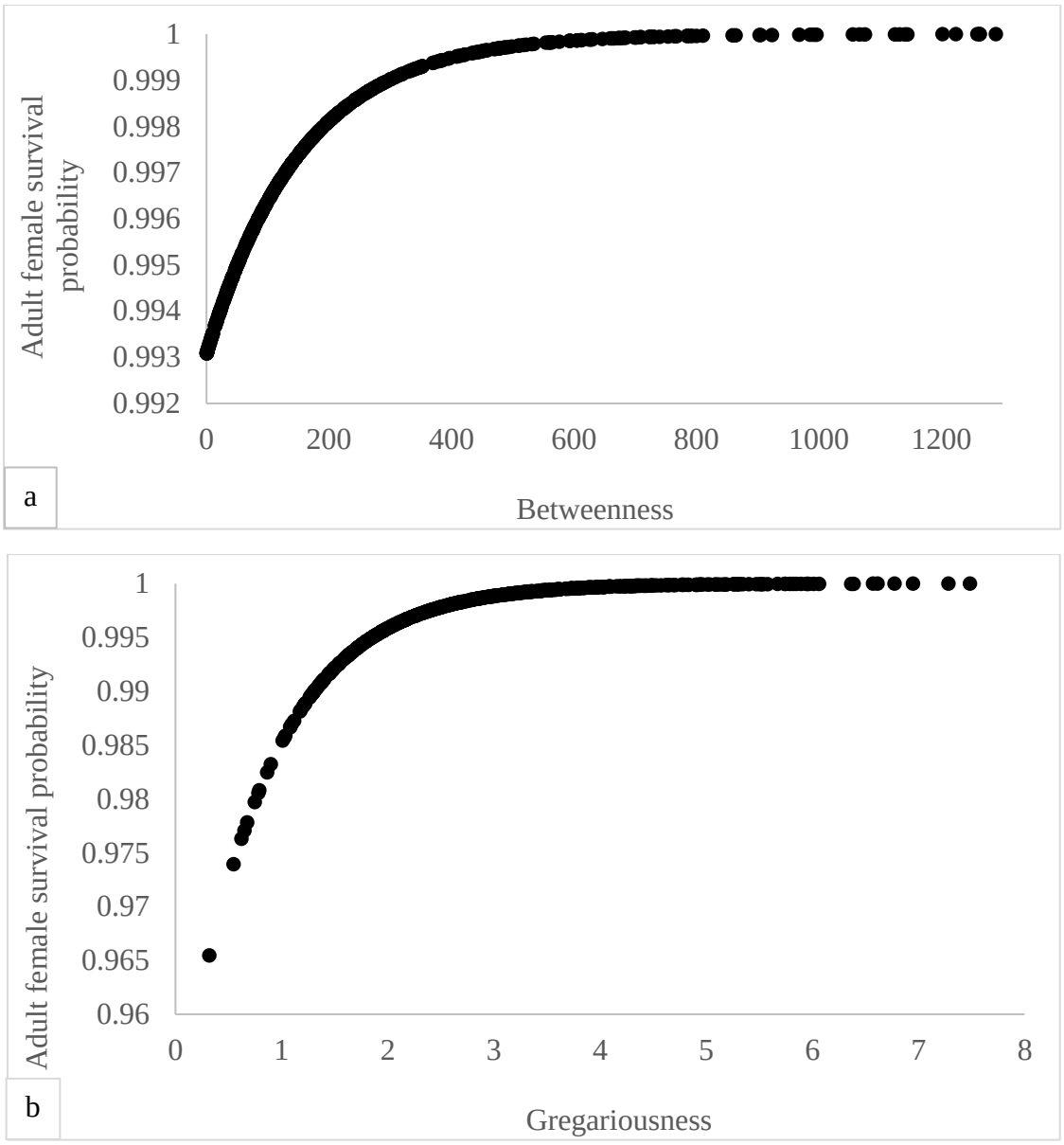

Figure 3. Relationship between (a) gregariousness and (b) betweenness and adult female giraffe survival probability.

Adult female survival probabilities increased and reached an asymptote once their average group size included approximately three other females. The maximum average gregariousness for an individual was to be with eight other females, but most females roamed in groups with two to five others (Supplementary Materials Fig. S1c). Survival probabilities improved in groups of three but gregariousness values did not exceed nine individuals, so our

results hint that there may be an optimal number of other adult female giraffes in a group. Environmental factors might constrain sociability so that there may be an upper limit to group sizes, for example competition for resources—especially during the dry season when food is limiting—or the presence of neonatal calves, or anthropogenic influences that disrupt social structure. Indeed, intermediate-sized groups of baboons have the lowest home range areas, average daily distances travelled, and average glucocorticoid concentrations for females, suggesting large groups suffer within-group competition whereas small groups face between-group competition and predation (Alberts et al. 2019).

Survival probabilities also increased when the number of paths flowing through the individual was greater than 700. Higher-betweenness animals are those that tend to change groups more often (Farine and Whitehead 2015) and have weaker ties with many other females rather than stronger ties with fewer others—corroborated by the relatively low average edge weights among individuals in our population, even among associated individuals (Bond et al. in press). Maryanski (1987) suggested that chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*) live in communities whereby weak ties between individuals can be advantageous because they facilitate movement across groups among familiar individuals, which, among chimpanzees facilitates a flexible feeding strategy focused on the dispersed distribution of fruits. Studies of both rhesus macaques (Ellis et al. 2019) and blue monkeys (Thompson and Cords 2018) also found that more well-integrated females with many weak ties had higher survival. The weak-tie system allows a greater number of individuals to connect with each other, be more socially integrated, and develop a sense of community but not a strong sense of subgroup affiliation as is indicative of more closed social systems, for example baboons (Silk et al. 2010).

Why would relatively moderate social bonds with multiple individuals be more adaptive than strong bonds with a few individuals? Grouping behaviour may increase adult survival for species where adults themselves are prey (e.g. Burchell's zebras, *Equus burchelli*, and blue wildebeests, *Connochaetes taurinus*, Thayer et al. 2010), as larger groups can better detect predators (Pulliam 1973) or deflect predation from themselves (Hamilton 1971). But adult female giraffes are far less vulnerable to natural predation than are calves, although females do bear a high prevalence of lion claw marks which were likely acquired during calf defense (Strauss and Packer 2013). Aside from poaching, the main culprits of adult female giraffe mortality are likely to be disease, stress, or malnutrition (Dagg 1971, Owen-Smith 2008), all of which are interconnected stressors. In a review of social influences on survival gleaned from long-term studies of baboons, Alberts (2019) noted that social relationships are used to manage intraspecific competition, predation, disease risk, and psychosocial stress, and to gain information about the environment. Female giraffes may be using social cues, seeking out, and joining with an optimal number of other females in order to obtain and monopolize the highest-quality food (Rieucau and Giraldeau 201), to lower stress levels by reducing male harassment as in feral horses (Cameron et al. 2009) or simply to experience physiological benefits by being around familiar females (Silk 2007).

Sharing information about the location and quality of food can improve foraging efficiency. Group-living animals can use social information from conspecifics to learn about the location and quality of a resource patch (Rieucau and Giraldeau 2011). Among giraffes, herd progressions are led nearly 80% of the time by the oldest female in the group, a pattern linked to learning about resource distribution by younger animals (Berry and Bercovitch 2014)

In many long-lived, iteroparous, polygynous ungulates, including giraffes, longevity is the most important determinant of female lifetime reproductive success (LRS)—the major component of fitness (Kjellander et al. 2004, Weladji et al. 2006, Bercovitch and Berry 2016). In most of these species, sex differences in longevity and breeding lifespan (Clutton-Brock and Isvaran 2007) are probably derived from the closer bonds that females have with conspecifics. Even weak social ties among females improves their reproductive success (e.g., baboons; McFarland et al. 2017). We suggest that many weak social ties formed by moving among groups, and roaming with an optimal number of others, improves the survival of adult female giraffes. Adult female giraffe associations are not particularly strong or stable in the short term (see e.g. Foster 1966, Leuthold 1979, Le Pendu et al. 2000, Bercovitch and Berry 2013), but females maintain long-term non-random bonds over their lifetime. Female giraffes across Africa have been shown to form complex multi-level societies, with preferred and avoided relationships even among individuals that share the same space (Carter et al. 2013a, VanderWaal et al. 2014, Bond et al. in press), and some associations persist over years (Bercovitch and Berry 2012, Carter et al. 2013b). Hence, despite the flexibility and short duration of most giraffe groups, the dynamics of their fission-fusion society is based upon the development of long-term social bonds among a subset of individuals within the community. Females vary substantially in their sociability, with higher levels of sociability and social integration associated with higher survival probabilities. Rather than strong social bonds with a few females, a flexible ability to form moderate bonds with many females within the community is associated with survivorship and probable LRS. In addition, sociability was more important to female survival than were various attributes of the physical environment.

Previous research in our population revealed that herd dynamics were adversely influenced by human activity, especially near traditional human settlements (bomas) (Bond et al. in press). At the same time, female giraffe groups with calves were more likely to be found closer to bomas (Bond et al. 2019) and reproductive rates (calves per adult female) were higher in communities closer to bomas (Bond et al. in review), which we attributed to reduced predator numbers or the interruption of predator behaviours as traditional pastoralists protected their livestock. In this study, distance to bomas or towns did not predict individual adult female survival, suggesting that those females who roamed in the optimal group size, even in areas close to human settlements, survived better than those that did not, but female giraffes seem to face a trade-off between their social relationships and their fitness.

As Aureli et al (2008) noted, fission-fusion social systems are not all identical, and a key component of giraffe fission-fusion societies is the formation of moderate social bonds within a structured community that increase the probability of survival, which is a key factor influencing their LRS. The flexibility in bond formation that females have evolved is probably associated with living in an environment with unpredictable resource distribution and abundance over the large home ranges that they must occupy in order to maximize reproductive success by maintaining a healthy body condition, while minimizing physiological stress by forming social ties with only a subset of others, thus forming discrete social communities. Social flexibility is an evolved adaptation among animals that provides individuals with the opportunity to adjust their foraging and reproductive strategies to maximize fitness in the face of unpredictable environmental conditions (Schradin et al. 2012). In the case of the African striped mouse, *Rhabdomys pumilio*, social flexibility can yield both group-living and solitary individuals (Schradin et al. 2012), while in the case of giraffes, social flexibility produces a fission-fusion

society that is characterized by variation in herd size and structure in response to demographic, environmental, and social factors that enable females to exploit "dispersed, unpredictable, restricted, and ephemeral food resources" (Bercovitch and Berry 2013). Our finding that survivorship is an outcome of social bonds emerging from individual social flexibility provides strong evidence that bonding is evolutionarily adaptive among giraffes and that giraffe have evolved a complex society.

Supplementary Materials

SIMPLE RATIO INDEX OF ASSOCIATION

Association indices are used to define edges in a network. They estimate the proportion of time nodes (individuals) are seen together, and range between 0 and 1, where 0 means two individuals were never seen together, and 1 means two individuals were always seen together. In the simple ratio index, the edge weight is calculated as: $E_{AB} = \frac{x}{x+y_{AB}+y_A+y_B}$, where E = undirected edge weight between individuals A and B, x = number of sampling periods where individuals A and B were observed in the same group, y_{AB} = number of sampling periods in which both A and B were observed but not together in the same group, y_A = number of samples where only individual A was seen, and y_B is the number of samples where only B was seen (Farine and Whitehead 2015).

SOCIAL COMMUNITY DETECTION

We began with a subsample of all adult females with at least six observations to improve the accuracy of the edge weights (Davis et al. 2018). A good module division provides many edges within communities and few between, and is quantified by a modularity coefficient known as Q (Newman 2003). We used the cluster-walktrap community-detection algorithm to divide the

adult female giraffe metapopulation into social communities and calculated modularity with package *igraph* for R (Csárdi and Nepusz 2006). We assessed the robustness of the community assignment using bootstrapping and the metric community assortativity (r_{com}), which takes into consideration the detectability of associations (Shizuka and Farine 2016). We calculated r_{com} with package *assortnet* for R (Farine 2016).

The cluster-walktrap community detection algorithm parsed the adult female giraffe metapopulation into 14 distinct communities with $Q = 0.742$, demonstrating a relatively high degree of modularity. A bootstrap test indicated the assignments of individuals to communities was robust ($r_{com} = 0.749$). The high Q and r_{com} values suggest strong community structure and high community fidelity with a low tendency for adult females to mix with other communities (Shizuka and Farine 2016).

Table S1. Spearman's correlation coefficients between social and physical environmental covariates for analysis of survival of 512 adult female Masai giraffes in the Tarangire Ecosystem, Tanzania (2012–2016). Degree = gregariousness. Strong correlations (≥0.50) in bold.

	Average edge weight	Maximum edge weight	Degree	Betweenness	Distance to boma	Distance to town	*A. drepanolobium*	*A. tortilis*	*D. cinerea*	Dense bushlands	Volcanic grasslands
Average edge weight	1										
Maximum edge weight	**0.54**	1									
Degree	**0.90**	**0.50**	1								
Betweenness	0.17	-0.17	0.14	1							
Distance to boma	0.16	0.23	0.14	-0.13	1						
Distance to town	-0.17	0.14	-0.16	-0.07	**0.57**	1					
A. drepanolobium	0.11	-0.08	0.16	0.02	-0.08	**-0.55**	1				
A. tortilis	0	0.06	-0.05	-0.10	0.05	0.31	**-0.59**	1			
D. cinerea	0.09	-0.12	0.14	0.15	-0.39	**-0.58**	**0.50**	**-0.60**	1		
Dense bushlands	0.12	0.23	0.10	-0.12	0.42	0.43	-0.38	0.28	-0.35	1	
Volcanic grasslands	0.10	-0.16	0.10	0.20	**-0.52**	**-0.77**	**0.53**	**-0.61**	**0.80**	-0.44	1

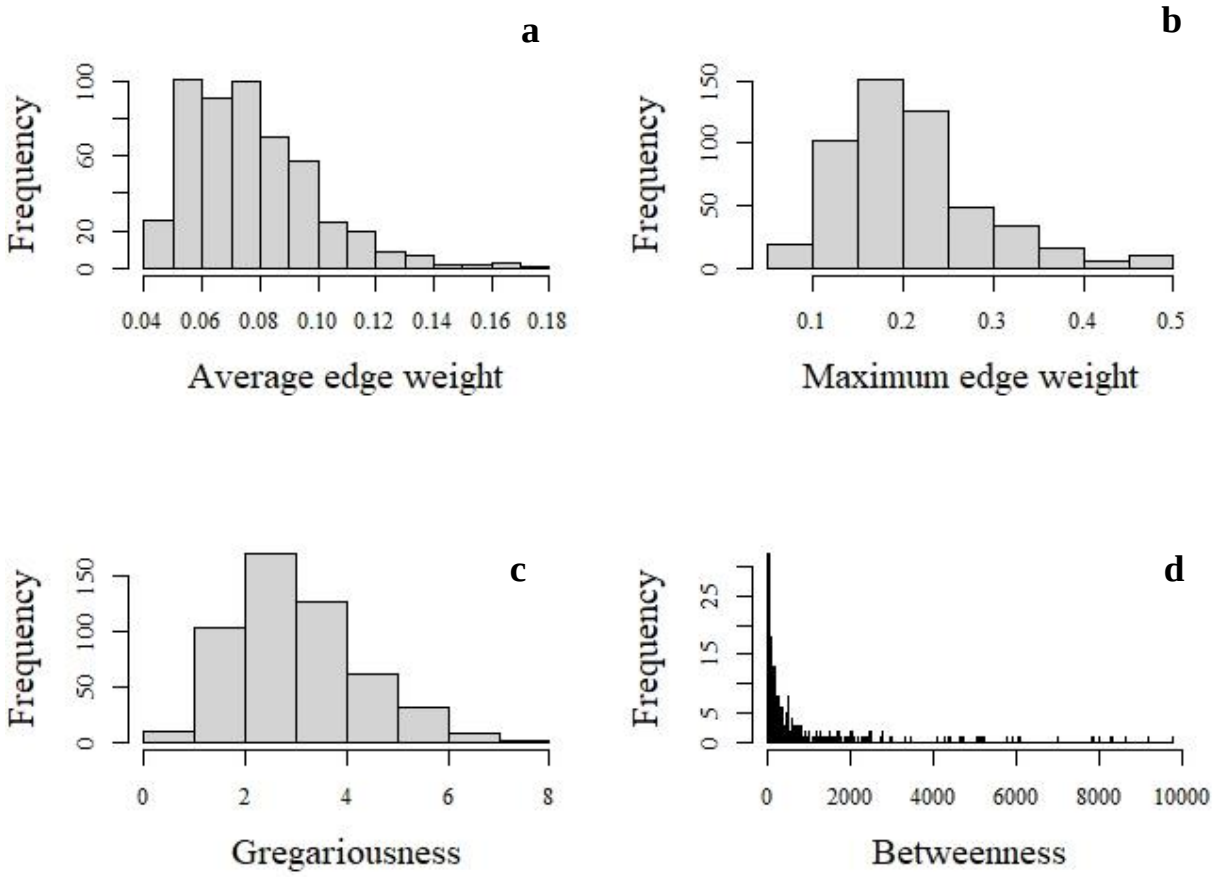

Figure S1. Histograms of the count of values for four measures of sociability among 512 adult female Masai giraffes: (a) average non-zero edge weight; (b) maximum edge weight; (c) average group size - 1 (gregariousness); and (d) betweenness.

Chapter 5

Leaving without going anywhere: Spatial versus social dispersal of juvenile giraffes

Monica L. Bond · Derek E. Lee · Arpat Ozgul · Damien Farine· Barbara König

Abstract

Natal dispersal is a critical process that influences population dynamics of wild animals. Sociality and the environment can influence dispersal patterns. For species that form discrete yet overlapping social communities, such as giraffes, natal dispersal might manifest as spatial (moving beyond a threshold distance while remaining in the natal community) or social (staying within a threshold distance while shifting to a different, overlapping social community) or both social and spatial (moving beyond a threshold distance and into a different community). Here we tested hypotheses about the influence of distance to low- and high-impact human settlements and local giraffe population density on probability and type of dispersal, dispersal distance, and age of dispersal in a metapopulation of free-ranging giraffes inhabiting a large, unfenced landscape. Both males and females dispersed at approximately 4 years of age. Young females rarely dispersed, and social dispersal by females was even more infrequent, confirming the importance of maintaining social ties with other females from calf to adulthood. Conversely, most young males dispersed, both socially and spatially, but 19% switched to a new social community without spatially dispersing. We suggest that overlapping social communities represent a pool of unrelated female mating partners in which males can avoid inbreeding while reducing the risks of traveling to unfamiliar areas. Social associations giving rise to discrete communities may represent an important element of fine-scale population structure in animal societies with multi-level organization.

Keywords dispersal, capture-mark-recapture, social network analysis, giraffe, *Giraffa camelopardalis*

Introduction

Dispersal influences individual fitness, gene flow, adaptation to local conditions, inbreeding, population size, colonization, and persistence of populations and species, and is a critical component in population dynamics (Devillard and Bray 2009). The natal dispersal process typically involves leaving the natal site or social group, traveling across unfamiliar territory, and settling in a new home range or social group to breed (Wolff 1994, Linklater and Cameron 2009). Dispersing individuals theoretically face higher risk of mortality than philopatric individuals because dispersers lack knowledge of habitat quality outside their natal range, and may face greater predation risk or experience stress from being without kin (Clobert et al. 2001). Dispersers most likely undertake these risks for the trade-offs of lower inbreeding probability and increased mating or social opportunities as well as potentially lower resource competition in the new location (Greenwood 1980, Wolff 1994, Linklater and Cameron 2009, Schradin et al. 2011). Dispersal distances and patterns should balance the costs and benefits of remaining versus leaving.

Sociality is another important component that influences dispersal patterns (Ekernas and Cords 2007, Blumstein et al. 2009, Linklater and Cameron 2009, Armitage et al. 2011). Many social mammal species frequently change their group sizes and compositions—called fission-fusion dynamics—with social structure arising from individuals forming close bonds with some and weak bonds with others (Kummer 1971, Whitehead and Dufault 1999, Whitehead 2008, Farine and Whitehead 2015). These dynamics lead to complex multi-level societies of smaller groups embedded within larger communities defined by more frequent associations among

individuals within than between communities (Newman and Girvan 2004). Sometimes discrete communities overlap substantially in space, with members of different communities occupying the same space at different times yet rarely or never seen together (e.g. Bond et al. in revision). These socio-spatial dynamics lead to the potential for juveniles to disperse to a new community near or even within much of the same spatial area used by their natal community, thereby reducing the costs associated with relocating to farther, unfamiliar areas while still allowing the formation of bonds with new individuals. This is termed 'social dispersal' as opposed to 'spatial dispersal,' and is evident in females of harem-forming equids with highly stable social groups (Linklater and Cameron 2009). Such social dispersal also may be theoretically possible in highly fission-fusion societies with discrete social communities, although this has not been investigated.

In mammals, juvenile males tend to disperse more than females, with females usually remaining close to their natal area and their female relatives (Greenwood 1980). However, younger females might benefit from leaving the social groups of their adult female relatives and forming their own groups, for example to reduce local competition for food resources (Schradin et al. 2011). The maintenance among adult females of many weak bonds that are stable over time is a feature of some primate social systems, including chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*; Maryanski 1987), and greater movements among groups and the formation of more weak ties was associated with higher survival of adult female giraffes (*Giraffa camelopardalis;* Bond et al. sociability). Therefore we might hypothesize that in multi-level mammalian social systems with high fission-fusion dynamics operating within discrete communities: (1) juvenile males exhibit longer-distance 'spatial dispersal' to entirely new areas where they are unlikely to inadvertently mate with their female relatives and (2) most juvenile males disperse, whereas (3) fewer juvenile females disperse and (4) most of those females that do

disperse exhibit shorter-distance 'social dispersal' into new social environments. We might further hypothesize that patterns of natal dispersal, such as whether or not they disperse and whether their dispersal is spatial or social, are influenced by environmental factors.

Here we test these hypothesis in a population of wild giraffes. Giraffes are long-lived (up to 30 yr), large (800–1200 kg), browsing ruminant ungulates that eat leaves, twigs, and fruits of woody savanna vegetation in sub-Saharan Africa (Dagg 2014). The giraffe is an ideal species with which to test hypotheses related to social versus spatial dispersal because adult females form discrete social communities, often overlapping in space (Bond et al. in press). Within these communities, group formations frequently merge and split in a fission-fusion process (Kummer 1971), but adult females show significant preferred and avoided associations with other females (Carter et al. 2013a, VanderWaal et al. 2014, Bond et al. in press), and females with preferred relationships are more closely related than those that appear to avoid each other (Bercovitch and Berry 2012, Carter et al. 2013b). Associations between males are less stable over time than between females (Carter et al. 2013a). Network analyses of a large metapopulation revealed more than 10 female-only communities that are discrete yet overlapping in space (Bond et al. in review comm demog), and 4 female-plus-male communities that are discrete and non-overlapping (Bond, unpublished data). These studies indicate giraffes exhibit a complex, structured social system characterized by multiple levels of organization.

Natal dispersal dynamics of giraffes are virtually unknown, and describing dispersal is an important step towards understanding the fine-scale spatial demographic dynamics for giraffes as well as other fission-fusion species with multi-level social systems. We investigated natal social dispersal using social network analyses (Whitehead 2008, Newman and Girvan 2004) and spatial dispersal using straightline distances from the first detection of the individual as a calf to each

subsequent detection (Börger and Fryxell 2012). We quantified age of dispersal, sex-specific natal dispersal propensity and type of dispersal (social or spatial), and distances moved from the first detection. We also developed and tested a suite of predictions about the influence of environmental factors on age, propensity, and distance moved. Previous research on dispersal in ungulates suggests an individual's choice towards dispersal or philopatry may be influenced by natal group density (red deer *Cervus elaphus*: Loe et al. 2009; feral horses *Equus ferus caballus*: Marjamäki et al. 2013), or by human presence (moose *Alces alces*; Singh et al. 2012).

Each giraffe has a unique coat pattern that does not change from birth to death (Foster 1966), enabling identification of individuals using non-invasive photographic mark-resight techniques, thereby producing large samples without the need for physical captures (Bolger et al. 2012). We used photographic identification data continuously collected over 7 years from a large giraffe metapopulation inhabiting 2200 km^2 in an environmentally heterogeneous, unfenced savanna landscape in northern Tanzania (Lee et al. 2016a, Lee and Bolger 2017). We analyse instances of dispersal and settlement and test our predictions for 70 juvenile females and 67 juvenile males that were born during the first two years of the study. Gaillard et al. (2008) considered a juvenile roe deer (*Capreolus capreolus*) to have dispersed if an individual moved more than the radius of an average adult home range size. The mean adult male giraffe home range size in our study area was 157.2 km^2 (Knüsel et al. 2019). Our study area size of 2,200 km^2 represents approximately 14 non-overlapping adult male home ranges, therefore we presume our study area provided adequate space to detect a range of dispersal movements.

We predicted the following:

(P1) We expected few juvenile females would disperse, and that most instances of female natal dispersal would be social rather than spatial, as this enables females to bond with more

individuals while remaining in familiar areas. However, we expected certain environmental factors might compel females to spatially disperse:

(P2) For females born closer to human settlements, dispersal probability would be higher, dispersal type would be spatial and thus distances travelled would be greater, and dispersal age would be lower due to habitat fragmentation, poaching risk, and behavioural disruption in those areas (Bond et al. in press).

(P3) Male dispersal distances would be greater and dispersal age would be lower for males born closer to human settlements, for the same reasons as P2.

(P4) Dispersal probability would be higher for calves born in communities with higher local giraffe population density (to reduce resource competition), although more giraffes could also signify good habitat or high-quality leader females, and offspring might therefore choose to remain in their natal community.

We also examined whether age at social or spatial dispersal differed between the sexes and was correlated with our selected environmental variables. Predation risk should not be a strong factor in dispersal probabilities or distances for giraffes because subadults and adults are far less vulnerable to predation than small calves (Strauss and Packer 2013).

Methods

STUDY AREA

The Tarangire Ecosystem in northern Tanzania is a heterogeneous landscape with varying degrees of anthropogenic pressures on wildlife, ranging from habitats deep within protected national parks to those in close proximity to towns (dense concentrations of concrete structures) and traditional homesteads of indigenous people, called bomas (dispersed family compounds of several huts constructed with natural materials). Bomas in our study area are occupied by

indigenous pastoralist Masai people who typically do not poach giraffes for meat, but may kill lions and other carnivores to protect livestock (Kissui 2008). Towns are much rarer, but also much more densely populated by people, typically surrounded by farmlands, and inhabited by bushmeat poachers who often target giraffes (Kiffner et al. 2015).

Vegetation types range from open grasslands to dense deciduous bushlands and thickets (Lamprey 1963). We sampled within a 2,200 km^2 area along road transects in four administrative areas with differing management activities (Fig. 1). Land management is partitioned among Tarangire National Park, Manyara Ranch Conservancy, and Mtowambu and Lolkisale Game Controlled Areas. Tarangire National Park has high levels of wildlife protection including exclusion of livestock and human settlements and rigorous anti-poaching patrols; Manyara Ranch has intermediate levels of wildlife protection with exclusion of human settlements and some anti-poaching patrols but with large numbers of livestock during the daytime. Portions of Lolkisale and Mtowambu Game Controlled Areas adjacent to Tarangire National Park have village Wildlife Management Areas with anti-poaching efforts similar to Manyara Ranch and exclusion of permanent human settlements permitted, but the remainder of the region has extensive sport hunting and permanent

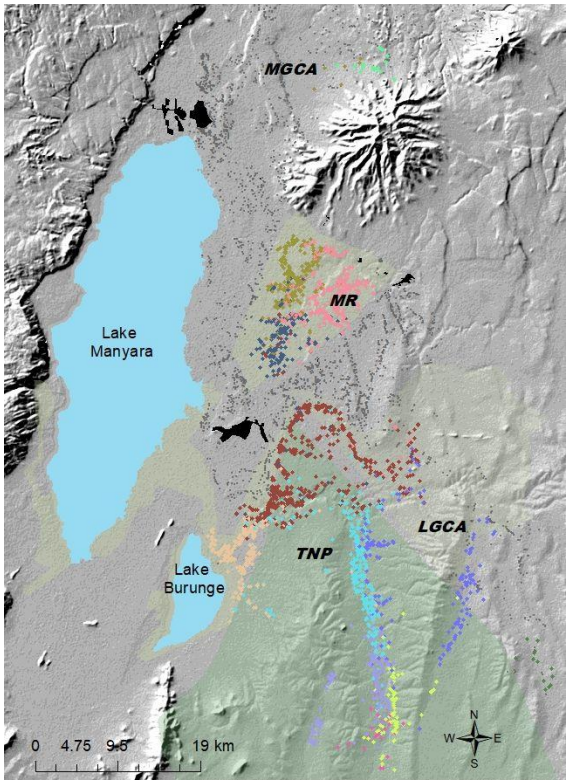

Figure 1. Locations of 12 adult female giraffe communities in the Tarangire Ecosystem of northern Tanzania, 2011–2016. TNP is Tarangire National Park, MR is Manyara Ranch Conservancy, MGCA is Mtowambu Game Controlled Area, and LCGA is Lolkisale Game Controlled Area. Green polygons are protected areas TNP, MR, and two community Wildlife Management Areas. Grey points are bomas, and black polygons are towns.

human settlements. All administrative areas are connected by movements of adult female giraffes (Lee and Bolger 2017).

The Rift Valley escarpment, a steep cliff that restricts giraffe movements, forms the western boundary of the study area. Wild large mammals are rarely observed east of Lolkisale Game Controlled Area and Manyara Ranch due to high human and livestock population densities, or southwest of Tarangire National Park due to widespread intensive agriculture. Two 2-lane asphalt roads cross the study area (Fig. 1).

FIELD DATA COLLECTION

We employed photographic capture-mark-recapture techniques to identify individual giraffes from the spot patterns unique to each animal (Foster 1966). We used the computer program Wild-ID to match patterns from photographs, which performed with little misidentification error in large giraffe datasets (Bolger et al. 2012).

We conducted 42 independent, daytime, fixed-route driving transect surveys to photograph giraffes between January 2012 and October 2018. The Tarangire Ecosystem experiences three precipitation seasons per year (short rains = Oct–Jan with an average monthly precipitation of 63 mm; long rains = Feb–May with 100 mm/mo; and dry = Jun–Sep with 1 mm/mo; Foley and Faust 2010). We surveyed for giraffes near the end of each of the precipitation seasons following a robust design with one primary sampling period composed of two independent, back-to-back secondary sampling periods during which we drove all transects in the study area (Pollack 1982). We sampled each track segment only one time each secondary sampling period. All survey roads were dirt tracks, and track density throughout the study area was high (0.42 km/km^2) relative to giraffe home-range size (115 km^2; Knüsel et al. 2019). All

surveys included the same two dedicated observers, and we maintained steady driving speed between 15 and 20 kph on all transects.

When we encountered giraffes, we 'marked or 'resighted' individuals by driving to within 150 m distance and photographing them. We recorded the following data for each giraffe: age class (calf, subadult, adult), sex (male, female), GPS location of the group, and distance from the camera to each giraffe (in meters) using a laser rangefinder (Bushnell Arc 1000; Overland Park, Kansas). We assessed a suite of physical characteristics, including body shape, relative length of the neck and legs, ossicone characteristics, and visual estimation of height to categorize giraffe into males and females and three age classes in the field: calf (<1 year), subadult (1–3 years), or adult (>3 years). We later used photogrammetry to objectively calculate age of calves to estimate approximate age of dispersal.

DATA ANALYSIS

Female giraffes in the wild typically first reproduce at 5–6 years old (Lee and Strauss 2016), but they become sexually mature at about 3.5 years, and males at about 4.5 years (Dagg 1971). Captive giraffes can become sexually mature as early as 2 years old for males, and 3 years old for females (Bingaman Lackey 2009). To ensure that we had resight data for at least 5 years after birth and thus a sufficient time period to detect natal dispersal, for our dataset of potential dispersers we considered only those individuals: (1) known to be calves in 2012 or 2013 (the first two years of the 7-year study) and (2) detected $\geq$6 times to improve accuracy of edge weights (Davis et al. 2018) and (3) detected at least once during each of 5 three-year time intervals: 2012–2014, 2013–2015, 2014–2016, 2015–2017, and 2016–2018.

For each detection in our dataset, we estimated size as a proxy for age. We used data from known age calves born in captivity to estimate age-specific neck length (NL), total height (TH),

and the ratio of NL/TH for giraffes aged 0 to 6 months. For images of our wild giraffes, we measured the number of pixels along the length of the giraffe's neck on all photographs. We used an algorithm incorporating the focal length of the lens and distance to the subject to convert pixels to cm and estimate NL and thus age when the first photograph was taken.

For social network analysis and constructing communities to examine social dispersal, we included the calf dataset above as well as all females first observed during the initial year of the study and (1) that were adults ($\geq$4 yr) the first time they were observed based on visual determination in the field, and (2) that were detected $\geq$6 times over the course of the study to improve accuracy of edge weights (Davis et al. 2018). We used the gambit of the group—individuals present together in the same group formation—to define associations between individuals (Whitehead and Dufault 1999). We defined a group formation as one or more giraffes that were foraging or moving together, and with >500 m distance to the closest member of another group (Carter et al. 2013a;b, VanderWaal et al. 2014, Bond et al. 2019). Our study design involved repeatedly measuring individually identified giraffes, with each individual assigned to only one group formation per primary sampling period, but with the same or a different set of individuals in groups during other primary sampling periods.

We then quantified which calves were philopatric and which dispersed, and which type of dispersal was evident. Overall, we classified individuals into four dispersal types based on social and spatial movements: (1) non-disperers; (2) social dispersers; (3) spatial dispersers; and (4) social and spatial dispersers (Fig. 2; see methods below for definitions).

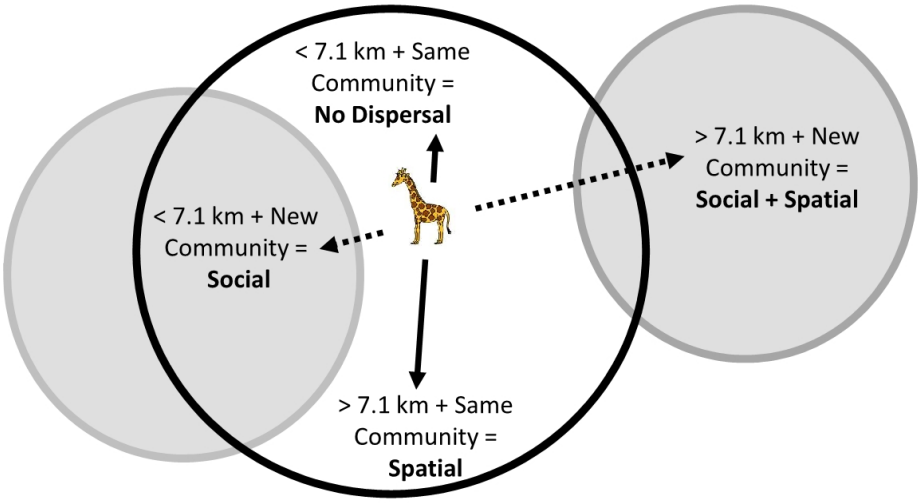

Figure 2. Types of dispersal of a hypothetical juvenile male giraffe in the Tarangire Ecosystem: Social dispersal is joining a new social community with dispersal distance < 7.1 km (radius of mean home range of adult male giraffes in this ecosystem) from first detection as a calf; Spatial dispersal is dispersal distance > 7.1 km while remaining in the natal social community; Social-and-spatial dispersal is dispersal distance > 7.1 km and joining a new social community; No dispersal is dispersal distance < 7.1 km and remaining in the natal community.

Social Dispersal—To investigate social dispersal, we created a social network with adult females, ran a community detection algorithm on the network, and tested robustness of our community detection using the approach and test statistic, r_{com}, described by Shizuka and Farine (2016). We calculated r_{com} with package *assortnet* for R (Farine, 2016). We then assigned each calf to a community for each of its detections based on majority membership of all the adult females in the calf's group formation at that detection. We then examined if and when the calf shifted to a different community. In some cases, the calf switched communities several times, which typically happened when the communities overlapped in space and adult females of different communities were found together in the same group formation. In these cases we assumed the calf was still with its natal associates. We differentiated among the following situations: (1) when the calf was always detected in the same community, social dispersal = 0; (2)

when the calf was detected in a community that was adjacent to or overlapping the natal community but then was detected subsequently thereafter back in the natal community, social dispersal = 0; (3) when the calf shifted to and was subsequently always detected in a community or communities that were different from the natal community, social dispersal = 1.

Spatial Dispersal—To investigate spatial dispersal, we calculated the straight-line distance between the first location and each successive location of the movement path of the animal (Turchin 1998). With this method we compared distance travelled by an individual over the course of our 7-year study relative to its first sighting as a calf, and considered the distance to the final location to be the dispersal distance (Fig. 3). We quantified each successive location's distance to determine when the animal made a "sortie" out of its natal range but then returned. Gaillard et al. (2008) classified dispersers as those that moved a threshold distance of more than the radius of an average adult home range. Following Gaillard et al. (2008), we considered a male to have spatially dispersed if they permanently moved a distance of more than 7.1 km (= radius of an average adult male giraffe home range size in our study area of 157.2 km^2) and a female to have dispersed if they moved a distance of more than 6 km (= radius of an average adult female giraffe home range size in our study area of 114.6 km^2; Knüsel et al. 2019). Individuals that conducted a "sortie" away from the natal location of more than the threshold distance, but then returned to within the threshold distance from the natal area, were not considered to be disperers.

Age of dispersal—We used photogrammetry to estimate age from heights, and assigned each calf an age in months for each detection. We attributed the age of social dispersal as the age at first detection in a community different from the natal community, and the age of spatial dispersal as the age at first detection at the threshold distance as described above. We only applied age of spatial dispersal for indviduals who moved the threshold distance, and we also calculated

age of first sortie. We also calculated age that an individual was first seen in a bachelor herd, which is defined as a group comprised of a majority of males.

Environmental correlates of dispersal—Lastly, we modelled dispersal probabilities, ages, and distances as functions of three environmental explanatory variables of the natal community: local giraffe population density, and distance to low- and high-impact human settlements. We used all the locations of all adult female community members to create a kernel home range for the community and calculate giraffe population density within the home range. We calculated 95% kernel home ranges using locations from all individuals in each community with the package *adehabitatHR* in R (Calenge 2006). Giraffe population density included all individual adult male and female giraffes ever detected in each community's home range (including overlapping communities), regardless of number of their detections. We calculated the average distance (km) from all locations of community members to the nearest boma (a low-impact human settlement constructed of natural materials by indigenous pastoralists for their families and livestock and surrounded by natural savanna) and the nearest town (a high-impact, densely populated human settlement, typically surrounded by farms). We used Google Earth imagery to map all bomas and towns, and to calculate distances we used the "Generate Near Table" function in the Analysis Tools toolbox in ArcMap.

To model factors influencing natal dispersal, we used linear regression models. We modelled three response variables for each individual: dispersal probability (0 or 1 for each of four dispersal types), approximate dispersal age (based on height), and dispersal distance (km). We modelled correlates of dispersal probability by type using multinomial regression with 'no dispersal' as the reference level, with package *nnet* in R (Venables and Ripley 2002). We modeled correlates of dispersal age and distance using linear regression with a Gaussian error

distribution. For model comparison, we used Akaike's Information Criterion corrected for small samples (AIC_c) and AIC_c weights in an information-theoretic approach (Burnham and Anderson 2002). We conducted model selection using package *MuMIn* (Bartoń 2019) and *AICcmodavg* (Mazerolle 2019) in R.

Results

Our dataset included 423 adult females and 137 potential dispersers (67 M and 70 F calves). We ran four community detection algorithms on the network of adult females. The highest modularity *Q* was the cluster-walktrap (0.689), followed by cluster fast greedy (0.667), cluster edge betweenness (0.661), and leading eigenvector (0.645). The cluster-walktrap algorithm parsed the adult females into 12 social communities (Fig. 1), and the bootstrap test revealed that our community assignment was robust (r_{com} = 0.765).

Dispersal Probability—(P1): We predicted fewer females would disperse, and that most instances of female dispersal would be social rather than spatial. We found that males were significantly more likely to disperse (Welch's two-sample t-test: t = 3.66, d.f. = 134.97, P < 0.001) and moved significantly greater distances from their origin than females (t = -3.2872, d.f. = 106.81, P = 0.001; Fig. 3). Of non-dispersers, 67% (n = 44) were females and 33% were males (n = 22). Of spatial dispersers only (not social dispersers), 68% were females and 32% were males, whereas social dispersers only (not spatial dispersers) were 81% males and 19% females. Of individuals who were both social and spatial dispersers, 80% were males and 20% were females. The majority of female calves did not disperse, either socially or spatially, supporting our prediction, but most of those that did disperse moved spatially while remaining within their natal community (Table 1), contrary our prediction. Most social dispersers were males (n = 37) compared to only 9 socially dispersing females.

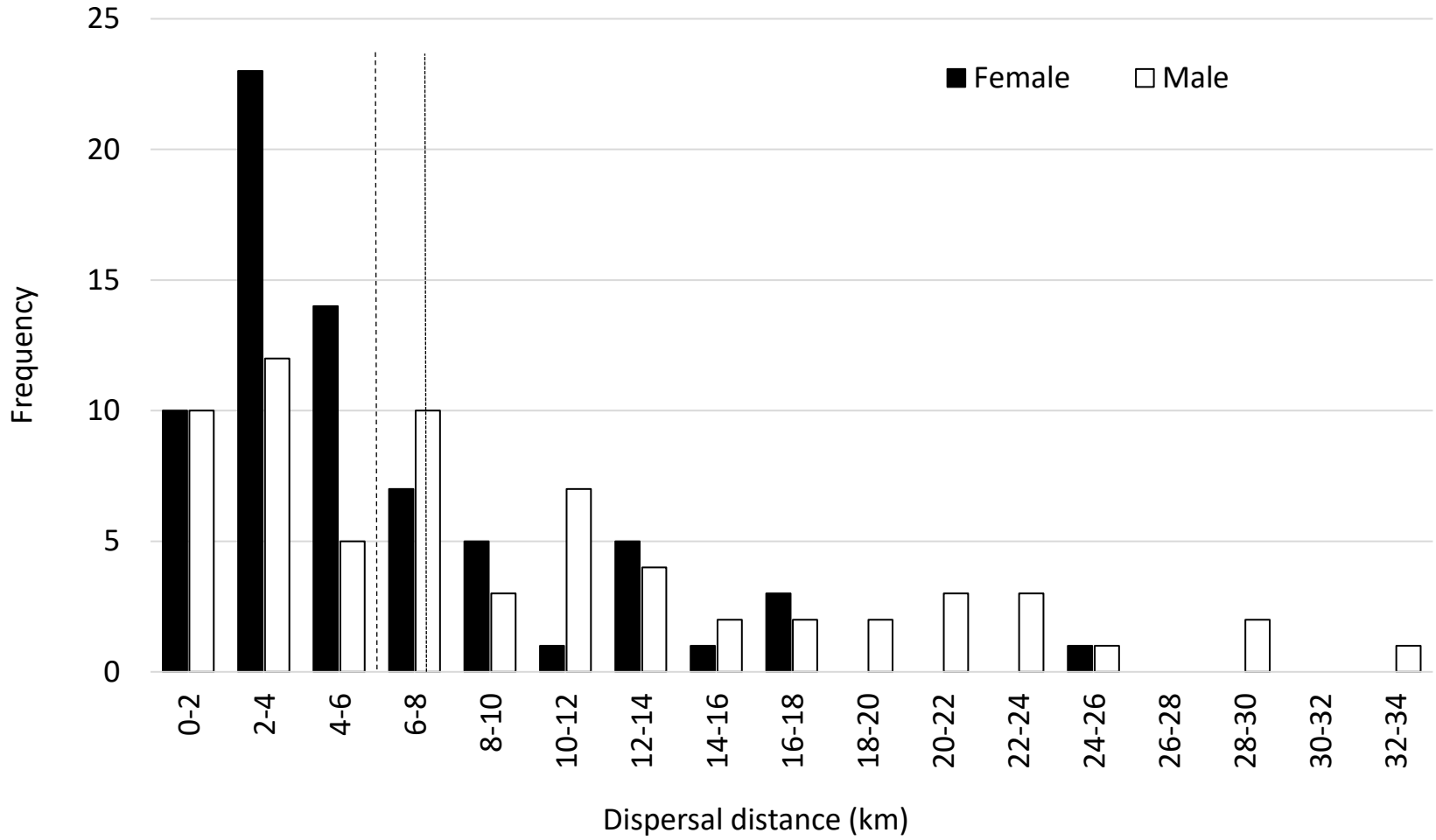

Figure 3. Histogram of dispersal distance (straight-line distance moved from first detection as a calf to last detection as subadult) in kilometers by frequency of individuals, for 137 male and female giraffes in the Tarangire Ecosystem, Tanzania, from 2012–2018. Dotted black line is the radius of the mean adult male home range size (7.1 km) and dashed black line is the radius of the mean adult female home range size (6 km) in this study area, from Knüsel et al. (2019). Individuals with dispersal distance greater than this radius were considered spatial dispersers.

Table 1. Summary statistics for proportion (*n*) of 67 male (M) and 70 female (F) giraffe calves in each dispersal class, mean dispersal distance, and maximum dispersal distance.

	No Dispersal	Social Dispersal	Spatial Dispersal	Social & Spatial Dispersal
Proportion Dispersal Class				
F	0.63 (44)	0.04 (3)	0.24 (17)	0.09 (6)
M	0.33 (22)	0.19 (13)	0.12 (8)	0.36 (24)
Mean Dispersal Distance (km)				
F	2.95	4.43	9.63	16.18
M	3.23	3.95	13.04	17.39
Max Dispersal Distance (km)				
F	5.80	5.86	16.29	26.14
M	6.90	6.56	19.21	32.85

Females conducted their first "sortie" at a significantly younger age than males (t = -6.1454, d.f. = 91.155, $P < 0.001$; Table 2). We assume long distances moved when the calf was < 6 months of age was a sortie with its mother. We found no difference between males and females in age at dispersal, either social (t = 1.0252, df = 12.298, $P = 0.325$) or spatial (t = -0.28663, df = 33.354, $P = 0.776$), nor did we detect a difference between the sexes in age first seen in a bachelor herd (t = -0.23218, d.f. = 11.784, $P = 0.820$). Both males and females dispersed either socially or spatially between about 45 and 52 months, or approximately 4 years of age (Table 2).

Table 2. Mean age (months) at first sortie (movement > the radius of an adult home range by sex), age first detected in a bachelor herd (group comprised of a majority of males), age of social dispersal, and age of spatial dispersal, for juvenile giraffes in the Tarangire Ecosystem, Tanzania, 2012–2018.

Sex	Mean First Sortie Age (*n* =104)	Mean First Bachelor Herd Age (*n* = 48)	Mean Social Dispersal Age (*n* = 43)	Mean Spatial Dispersal Age (*n* = 53)
F	17 (11) *n* = 51 range 2–50	39 (15) *n* = 8 range 26–66	52 (19) *n* = 9 range 22–73	45 (24) *n* = 21 range 8–78
M	34 (17) *n* = 53 range 4–74	40 (18) *n* = 40 range 6–88	45 (18) *n* = 34 range 12–74	47 (17) *n* = 32 range 19–78

Environmental Correlates of Dispersal—(P2) and (P3): We predicted females and males born closer to human settlements would be more likely to spatially disperse, dispersal distances would be greater, and dispersal ages would be lower. We also expected that calves born in communities with higher local giraffe population densities would be more likely to disperse (P4).

For our multinomial model of sex and environmental covariates in which the response variable was probability of being one of four types of disperser (no dispersal, social only, spatial only, social and spatial), we found probability of being a social-only disperser ($\beta_{sexSO} = 3.169$, $P = 0.002$) or a social-and-spatial disperser ($\beta_{sexSS} = 3.853$, $P = < 0.001$) was significantly higher for males. Relative risk ratios (exponents of the coefficients) indicate that males were > 9 times more likely to socially disperse and > 8 times more likely to socially-and-spatially disperse than females. Calves born closer towns were significantly less likely to be social-and-spatial dispersers than to not disperse ($\beta_{townSS} = 2.255$, $P = 0.024$). The relative risk ratios indicate that for each kilometer a calf was first detected away from a town, that calf is 1.19 times more likely to be a social-and-spatial disperser. Calves born in communities with higher population densities were less likely to spatially disperse than to not disperse ($\beta_{popdensSP} = -2.292$, $P = 0.022$).

We ran a subset of five *a priori* models to test the effects of various additive and interactive combinations of distance to boma, distance to town, and population density environmental covariates as well as sex (1 = male, 0 = female), on two continuous response variables: distance moved from origin (dispersal distance) and dispersal age (Table 3). Distance to boma and distance from town were negatively correlated (correlation coefficient = -0.89) so we did not include these two variables together in any models. We conducted model selection to assess which model in our set best fit the data.

The top-ranked dispersal distance model indicated that males moved greater distances than females ($\beta_{sexDist}$ = 3.645, $P < 0.001$; Table 4). Distance of natal area to towns was positively correlated with dispersal distance, meaning the farther an individual was born from a town, the farther their dispersal distance ($\beta_{townDist}$ = 0.267, $P < 0.001$; Table 4 and Fig. 4), but population density was not a significant effect ($\beta_{popdensDist}$ = -0.472, P =0.207; Table 4). The top model explained 20% of the variation in dispersal distance (adjusted R^2 = 0.201) and carried 66% of the weight in our candidate model set (Table 3).

None of our environmental covariates were significantly correlated with dispersal age. Dispersal age also did not differ between the sexes (conditional model-averaged β_{sexAge} = 1.412, 95% confidence interval = -10.335–13.157, P = 0.812; Table 4). Finally, we found no significant effects of local giraffe population density on dispersal distance or dispersal age (Table 4).

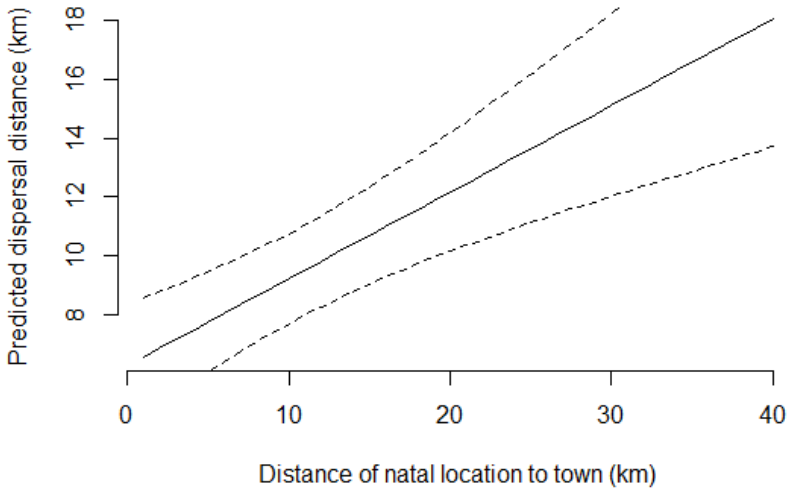

Figure 4. Predicted dispersal distance, the straightline distance between first and last detections, as a function of distance of natal location to the nearest town.

Table 3. Model selection results ranking 5 linear regression models explaining variation in dispersal distance, the straightline distance (km) from first to last location, and age of dispersal (months) for giraffe calves in the Tarangire Ecosystem of northern Tanzania, 2012–2018, based on maximum likelihood estimation.

Dispersal Distance Models	(Intercept)	Dist Town	Pop Dens	Sex	Dist Town * Sex	Pop Dens * Sex	Dist Boma	Dist Boma * Sex	d.f.	logLik	AICc	ΔAICc	Weight
Sex+DistTown+ PopDens	5.32	0.27	-0.47	+					5	-443.97	898.40	0.00	0.66
Sex+DistTown+ PopDens+Sex*DistTown+ Sex*PopDens	5.43	0.16	-0.26	+	+	+			7	-442.45	899.76	1.36	0.33
Sex+PopDens	10.81		-1.11	+					4	-450.33	908.97	10.57	0.00
Sex+DistBoma+PopDens	9.48		-0.98	+			0.17		5	-449.81	910.08	11.68	0.00
Sex+DistBoma+PopDens+ Sex*DistBoma+ Sex*PopDens	7.50		-0.48	+		+	0.11	+	7	-448.49	911.86	13.46	0.00
Dispersal Age Models													
Sex+DistTown+PopDens	50.52	-0.63	0.68	+					5	-230.16	471.60	0.00	0.56
Sex+PopDens	36.31		2.41	+					4	-232.34	473.51	1.91	0.22
Sex+DistBoma+PopDens	42.23		1.91	+			-0.80		5	-231.57	474.41	2.81	0.14
Sex+DistTown+PopDens+ Sex*DistTown+ Sex*PopDens	63.71	-0.85	-2.21	+	+	+			7	-229.63	475.74	4.14	0.07
Sex+DistBoma+PopDens+ Sex*DistBoma+ Sex*PopDens	49.05		-0.46	+		+	0.48	+	7	-231.00	478.49	6.89	0.02

Table 4. Estimates from top-ranked model for dispersal distance, and from conditional model averaging for dispersal age. Parameter estimates, standard errors, t or z-values, and *P* values are from multiple linear regression models explaining variation in dispersal distance and dispersal age for giraffe calves in the Tarangire Ecosystem of northern Tanzania, 2012–2018. Bold indicates significant effects ($P < 0.05$).

Dispersal Distance				
	Estimate	SE	t value	Pr(>|t|)
(Intercept)	5.311	2.261	2.349	**0.020**
Sex (M)	3.645	1.088	3.351	**0.001**
DistTown	0.267	0.074	3.598	**0.000**
PopDens	-0.472	0.372	-1.269	0.207
Dispersal Age				
	Estimate	Adj SE	value	Pr(>|z|)
(Intercept)	45.911	11.422	4.020	**0.000**
Sex (M)	1.411	5.993	0.235	0.814
DistTown	-0.630	0.316	1.997	0.046
PopDens	1.273	2.034	0.626	0.531
DistBoma	-0.804	0.685	1.173	0.241

Discussion

We used a 7-year dataset of 137 male and female giraffe calves in a large (2,200 km^2) unfenced, ecologically heterogenous study area in the first-ever investigation of natal dispersal of this iconic megaherbivore. We proposed juveniles could disperse either socially (to a new social community) or spatially, or both, and tested whether propensity to disperse, type of dispersal, age at dispersal, and distance traveled would be correlated with anthropogenic factors and giraffe population density in the natal social community. Male and female giraffes showed significantly different patterns of dispersal. We found young male giraffes were more likely to disperse, and dispersed greater distances, than females. Contrary to our prediction, females rarely dispersed socially. If females dispersed at all, they moved beyond the threshold distance we considered to be spatial dispersal (6 km) while remaining in their natal social community; fewer than 13% of females joined new communities. If males dispersed, they were most likely to move farther distances and into new communities, although 19% of males switched to a new social community

without moving beyond the threshold for dispersal (7.1 km). Overall 55% of males dispersed socially. Both males and females dispersed from either their natal area (spatial dispersal) or natal community (social dispersal)—or both—at approximately 4 years of age. Calves born in communities with higher local giraffe population densities were less likely to spatially disperse.

We also found an anthropogenic influence on type of dispersal as well as distance traveled. Individuals born closer to towns were less likely to be social-and-spatial dispersers and did not move as far from the location where they were first detected as calves. Dispersal age was not influenced by any environmental factors.

Not surprisingly, the majority of female giraffes remained 'at home.' A smaller proportion dispersed spatially, but very few females showed evidence of social dispersal. Although we had predicted otherwise, the lack of female social dispersal makes sense in the context of the fitness importance of maintaining many ties among all members of the community (Bond et al. sociability). Here, we had expected dispersing females to remain close to their natal area within familiar habitat, but form new ties with members of a different community. However, we found the opposite, whereby dispersing females moved away spatially from their natal area but maintained associations within their natal community. Thus, the drive to continue associating with familiar individuals likely encourages females to 'stay at home', either by settling near the natal area or within the natal community. However, a small proportion of females did move relatively long distances away, and an even smaller proportion switched social communities. What factors might impel a young female to move away from the social community in which she was born and raised? Long-term research on marmots (*Marmota flaviventris*) documented that female yearlings that interacted with more others and were more socially embedded with their groups were less likely to disperse (Blumstein et al. 2009). Further, when the mother was present

and the young female showed more amicable behaviors towards its mother and other yearling females, dispersal was less likely (Armitage et al. 2011). Intenstive sampling of female giraffe calves and subadults to obtain estimates of sociability may reveal that giraffe females that are more integrated in their communities are less likely to socially or spatially disperse.

We have clearly demonstrated that the maintenance of bonds among female giraffes within their social community, from calf to adult, is an important feature of female giraffe societies. Bond et al. (in review) documented that adult female social communities in the Tarangire Ecosystem comprised approximately 60–90 individuals, with many of the community home ranges overlapping substantially despite individuals remaining discrete in their associations. Carter et al. (2013a) showed that female giraffes with 'preferred' relationships were more related to each other than expected from random associations, and avoided unrelated females. We therefore suspect that relatedness may be an underlying factor in forming socially discrete communities of associates, resulting in the complex multi-level social organization evident in this highly fission-fusion species.

Young male giraffes, on the other hand, were more likely to 'leave without going anywhere' than females via social but not spatial dispersal, although most males still dispersed both spatially and socially. The majority of males dispersed socially, supporting the notion that discrete social communities—even those that overlap in space—are a biologically meaningful basis for fine-scale population structure that contributes to metapopulation dynamics across a landscape (Bond et al. in review). If adult female social communities indeed arise from genetic relatedness, males may be able to seek unrelated mating partners and avoid inbreeding without the need to disperse long distances into unfamiliar areas, simply by shifting to a new, nearby social community.

The fact that one-third of males did not disperse at all was surprising, but our sample of males likely represents a transition stage from calf to subadult. Male giraffes can become sexually mature at approximately 4.5 years of age (Dagg 1971), but likely do not successfully mate until an older age in the wild. In contract to the tallest, oldest bulls with prominent bone structures on the forehead—indicative of mature, dominant males—subadult male giraffes ($\leq$ 4 yrs) and younger mature bulls in a South African population had higher fecal glucorticoid levels associated with "puberty" (Wolf et al. 2018). High glucorticoid levels indicated they were still subordinate to the dominant bulls. Therefore, it is possible that with additional years of data, more of the young males in our study area that did not disperse might eventually move away from the females to whom they are related, once they can challenge other bulls in the dominance hierarchy. In contrast, with our 7-year dataset, our sample of females was old enough to begin reproducing by the last time period in our study, thus we presume our results represent females that have settled into their final breeding areas and social communities.

Our results differ markedly from the only other ungulate species where social versus spatial dispersal was examined, the feral horse (*Equus caballus*; Linklater and Cameron 2009). Mares dispersed from their natal groups coinciding with their sexual maturation, but groups into which they dispersed were predicted by proximity to the mare's natal group (Linklater and Cameron 2009). Thus, mares appeared to exhibit social but not spatial dispersal. However, horses are unusual in that both males and females disperse from their natal groups and form or join groups with unrelated individuals (Cameron et al. 2009). Furthermore, equid populations have stable group membership whereas giraffes live in a highly fission-fusion society with group membership changing frequently (Leuthold 1979, Bond et al. 2019). Such a socially dynamic society likely necessitates constant maintenance of social ties across the community of others with

whom an individual is likely to come into contact (Bond et al. sociability). Giraffe dispersal patterns are similar to other polygynous ungulate species in that they tend to have female philoptray and male dispersal (Dobson 1982), but our research adds a new layer of understanding to the dynamics of social versus spatial dispersal, demonstrating that most young males disperse socially while young females rarely do.

Contrary to our expectations, individuals born farther from towns, deep in the heart of the protected areas, were likely to move greater distances and into new communities when they dispersed. One possible explanation is that giraffe communities occupying vast intact habitats within protected areas may have a lower degree of spatial overlap, thus compelling individuals seeking to disperse to new communities to travel farther distances. Indeed, in a previous analysis two of Tarangire National Park's giraffe communities situated >10 km from the nearest town also had relatively low degrees of overlap with other communities (Bond et al. in review Tables 1 and S2). Further, we found that calves were less likely to spatially disperse when born into communities with higher local giraffe densities, suggesting that giraffes congregate in quality habitat, and that these higher-density communities are below carrying capacity for density-dependence to impel spatial dispersal. The three communities with the highest giraffe population densities were in Manyara Ranch (Fig. 1) which has more-fertile volcanic soils relative to the soils in southern and central Tarangire National Park (Bond et al. in revision). Communities in the northern part of our study area, including Manyara Ranch and northern Tarangire National Park also had relatively higher reproductive rates (Bond et al. in review Fig. 2). The high giraffe population densities and high reproductive rates indicate apparently high-quality habitat, but at the same time these communities are closer to towns, which may explain why young giraffes born in these communities tended not to disperse. It is also possible that this current study suffers

from a spatial sampling bias whereby some animals near the edge of our study area—closer to towns—were more likely to disperse outside of our survey boundaries, although suitable habitat outside protected areas is sparse around towns; our sample may therefore include only those individuals who chose to remain close to the natal area. Our study area contains most of the suitable giraffe habitat in the region, thus we expected most animals to remain within our survey boundaries, but dispersal into outerlying areas, such as JKT Ranch to the northeast, Simanjiro to the east or Selela to the north, potentially does occur. Conducting additional surveys to identify giraffes in these outerlying areas could find longer-distance dispersers originating from areas near towns.

CONCLUSIONS

To our knowledge, our classification of individuals into social versus spatial dispersers using social network analysis and community detection is a novel technique to investigate dispersal patterns of a free-ranging animal. We have previously reported variation in demographic rates of adult and calf survival and reproduction among these communities, and here we show that spatially overlapping social communities can act as a pool of potential new unrelated mates for young males, even as they remain close to their natal area. Our unique dataset of hundreds of individuals roaming over multiple years across a large, unfenced, connected landscape supporting a dozen overlapping social communities provided an excellent opportunity to investigate social versus spatial dispersal, and elucidate potential environmental factors that mediate different types of dispersal. Understanding the patterns and drivers of the dispersal process is key for predicting how dispersal influences population dynamics, and is particularly important for effective conservation of endangered species such as the giraffe (Muller et al. 2018).

Chapter 6

Correlates of home range sizes of giraffes in a human-natural landscape

Mara A. Knüsel · Derek E. Lee · Barbara König · Monica L. Bond

Published in *Animal Behaviour* (2019) 149, 143–151. doi.org/10.1016/j.anbehav.2019.01.017

Abstract Abiotic, biotic and human influences are factors that can affect animal home ranges. We calculated home range sizes of adult giraffes in the Tarangire-Manyara region of northern Tanzania (N = 132 giraffes with data collected over 6 years), and investigated correlations between home range sizes and environmental and anthropogenic factors (for a subset of N = 71 giraffes). We used a 95% kernel utilization distribution to define home ranges and modelled home range size as a function of environmental and anthropogenic predictors using multiple linear regression and model selection. We also computed home range sizes of giraffes using 100% minimum convex polygons to compare with estimates from previously published studies, and tested the relationship between rainfall and home range sizes of giraffes across Africa. Average kernel home range sizes were 114.6 km^2 for females (N = 109) and 157.2 km^2 for males (N = 23). Adult female giraffe home range sizes (N = 67) were negatively correlated with distance to densely populated towns. Females living closer to towns had significantly larger home ranges, suggesting a need to range farther to avoid human-impacted areas while obtaining critical resources. No such relationship was evident with bomas, which are homesteads built by indigenous pastoralist people, suggesting that female giraffes are tolerant of traditional land uses. Mean annual rainfall explained 74% of the variation in home range sizes of giraffes across the African continent, with smaller home ranges in regions with higher rainfall and thus greater productivity, providing additional evidence that access to critical resources mediates home range size of this megaherbivore. Quantifying home range sizes and identifying ecological and

anthropogenic factors affecting space use can provide insights into mechanisms driving use of space and help wildlife managers make informed decisions that improve conservation plans for at-risk species such as giraffes.

Keywords *Giraffa camelopardalis*, giraffe, home range estimation, kernel utilization distribution, minimum convex polygon

Introduction

An important concept that describes space use by animals is the home range, the spatial extent over which an animal repeatedly travels in search of food and mates and to care for young (Burt, 1943). Home range behaviour is assumed to be an expression of an animal's decision-making process, shaped by natural selection, to access spatially dispersed resources in a manner that increases fitness (Börger et al., 2008; McLoughlin et al., 2007; Mitchell & Powell, 2004; Powell & Mitchell, 2012; Schoepf et al., 2015). Landscapes tend to be spatially heterogeneous, so the amount of space used by an individual is partially dependent upon the type, abundance and composition of resources across the landscape (Dechen Quinn et al., 2013; Ofstad et al., 2016; Saïd & Servanty, 2005). Energy is required to access those resources; therefore, space use consists of a trade-off between acquiring resources and expending energy (Fretwell & Lucas, 1970). Overall, animals theoretically should occupy the smallest area that contains the required resources (Harestad & Bunnell, 1979).

Ungulates are a diverse group of large herbivores that have a profound impact on plant populations, vegetation structure and ecosystem processes (Ofstad et al., 2016). The structure and function of East African savannah ecosystems are reliant upon intact communities of ungulates, as these mammalian herbivores consume about half of all plant production and are important prey for predators and scavengers (du Toit & Cumming, 1999; Shorrocks, 2007). However, most

studies of ungulate home range ecology are from temperate regions (Ofstad et al., 2016). Home range sizes of ungulates in temperate regions are influenced by biotic factors including the configuration of habitat within the landscape (Cibien & Sempere, 1989; Saïd et al., 2005; Saïd & Servanty, 2005; Tufto et al., 1996), an individual's sex, age (Cederlund & Sand, 1994; Relyea et al., 2000) and body weight (Harestad & Bunnell, 1979), and by abiotic factors such as climate and season (Morellet et al., 2013), the species' local population density (Kjellander et al., 2004) and human impacts (Dechen Quinn et al., 2013). Quantifying biotic and abiotic drivers of home range behaviour of ungulates in African savannahs can advance our understanding of tropical species and the elements they require to survive and reproduce. In addition, by quantifying home range sizes and identifying ecological and anthropogenic factors affecting space use, wildlife managers can make informed decisions that improve conservation plans for at-risk species (Deacon & Smit, 2017).

Giraffes, *Giraffa camelopardalis*, are endemic African ruminant ungulates, and one of only a handful of extant terrestrial megaherbivore species (Owen-Smith, 1988). Giraffes are nonterritorial, resident browsers that feed mostly on leaves, twigs, flowers and fruits of woody plants (Dagg, 2014). The species plays a major role in shaping the vegetation of savannah ecosystems (Strauss et al., 2015). Africa-wide, most populations of giraffes have declined in recent decades (Muller et al., 2018). Quantifying spatial ecology and landscape use by giraffes is critical for developing effective conservation measures (Deacon & Smit, 2017). Several studies have reported home range sizes for giraffes throughout the species' range (Berry, 1978; Deacon & Smit, 2017; du Toit, 1990; Fennessy, 2009; Le Pendu & Ciofolo, 1999; Leuthold & Leuthold, 1978; van der Jeugd & Prins, 2000), but these estimates varied substantially (Table 1). Abiotic, biotic and human influences are likely to be contributing factors that affect home range sizes of

giraffes, yet ecological and anthropogenic influences that might underlie giraffe space use have not been quantitatively analysed.

Our first objective was to calculate year-round home range sizes of adult Masai giraffes, *G. c. tippelskirchi*, from a free-ranging population in the Tarangire-Manyara Ecosystem of northern Tanzania. This ecosystem consists of a mix of vegetation types, as well as of protected and unprotected lands.

Second, we examined correlations between individual home range size and environmental and anthropogenic factors at an ecosystem scale in a spatially heterogeneous study area (~1500 km^2) to better understand potential mechanisms driving space use of this threatened megaherbivore. We specifically tested whether giraffes with a greater amount of closed habitat in their home ranges have smaller home range sizes, as denser vegetation offers both food and cover (Ofstad et al., 2016). We also predicted that home range sizes of giraffes living closer to human habitation would be larger because the human-impacted landscape in this study area is fragmented by agriculture and fuelwood cutting (Msoffe et al., 2011) and bushmeat poaching is widespread (Kiffner et al., 2015). Finally, we tested whether males had larger home ranges than females as their life-history strategy involves roaming among herds seeking adult females in oestrus (Dagg, 2014). Home ranges can change due to factors such as seasonal movements (Morellet et al., 2013), so it is important for robust analyses to ensure that home range estimates have stabilized. Therefore, we performed a bootstrap procedure to assess home range stabilization given each individual's sample size of locations and used only the subsample of giraffes whose home range estimate stabilized (Tingley et al., 2014).

Our third objective was to compare home range estimates from our study area with published data from giraffe populations across Africa, and to test the relationship between giraffe

home range size and mean annual rainfall at the continental scale as a potential explanation for observed variation in space use among populations.

Methods

STUDY SITE

The study area was located in northern Tanzania, East Africa. We sampled a 1500 km^2 area that included parts of Tarangire and Lake Manyara National Parks and the entirety of Manyara Ranch Conservancy (Fig. 1). The 2850 km^2 Tarangire National Park is the largest protected area in the region (Lamprey, 1963). Our giraffe survey area encompassed the northern half of the park. Manyara Ranch Conservancy, located 3 km north of Tarangire National Park, is a private 140 km^2 ranch dedicated to tourism and habitat conservation. Lake Manyara National Park, in the west of the study area, spans a 330 km^2 area between the alkaline Lake Manyara and a steep rift wall, of which we surveyed the northern two-thirds. The mean altitude of the region is approximately 1000 m above sea level.

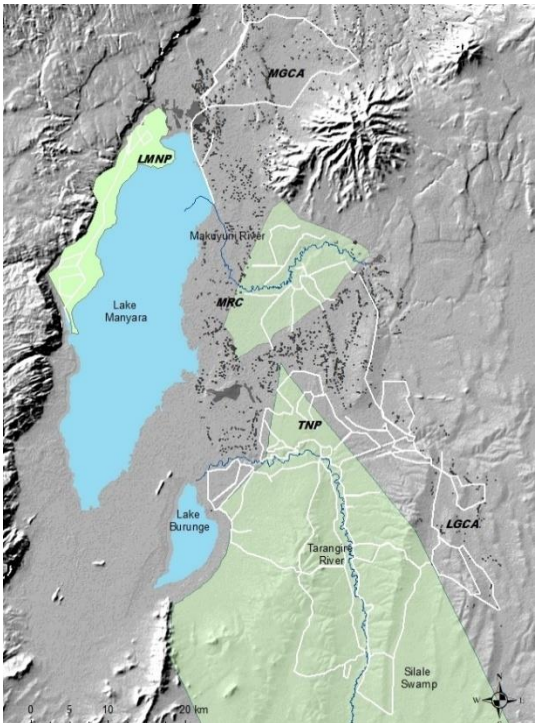

Figure 1. Study area in the Tarangire-Manyara Ecosystem of northern Tanzania. White lines are roads and tracks surveyed for Masai giraffes, *G. c. tippelskirchii*, blue lines are rivers, light blue areas are alkaline lakes, green areas are national parks and conservancies, grey polygons are towns and points are bomas. LMNP = Lake Manyara National Park; TNP = Tarangire National Park; MRC = Manyara Ranch Conservancy; MGCA = Mtowambu Game Controlled Area; LGCA = Lolkisale Game Controlled Area.

The study area consists of a savannah biome with variation in vegetation types ranging from open grasslands to dense deciduous bushlands and thickets (Lamprey, 1963). The Makuyuni and Tarangire Rivers and associated waterholes, together with several streams flowing down the

rift wall into Lake Manyara, provide year-round access to water for wildlife. The landscape connecting the three reserves is fragmented by roads, villages and agricultural land, but the study population of giraffes is still considered a functioning metapopulation as all reserves are connected by movements of adult females (Lee & Bolger, 2017).

DATA COLLECTION

Giraffe locations—During 2011–2016, we conducted 31 photographic capture–recapture surveys during which we systematically searched for giraffes along all dirt roads in the study area. Each sampling occasion consisted of two back-to-back surveys (surveys were done by M.L.B. and D.E.L.), or sampling events, conducted towards the end of every precipitation period (short rains = February; long rains = June; dry = October) and separated by 4-month intervals. During each sampling event, individuals were either 'captured' or 'recaptured' by slowly approaching and photographing the animal's right side from approximately 150 m at a perpendicular angle (Canon 40D and Rebel T2i cameras with Canon Ultrasonic IS 100–400 mm lens, Canon U.S.A., Inc., One Canon Park, Melville, New York, NY, U.S.A.). We identified individual giraffes from the photographs using their unique and unchanging coat patterns (Dagg, 2014; Foster, 1966) with the aid of pattern-recognition software Wild-ID (Bolger et al., 2012). We also recorded every individual's geographical coordinates, sex and age class. We used several physical characteristics to categorize giraffes into the three age classes: calf, subadult or adult (adults were at least 3 years old, according to Strauss et al., 2015). Successive relocation points were separated by ≥10 days; thus, we expected minimal autocorrelation for home range estimation (Fieberg, 2007).

ENVIRONMENTAL AND ANTHROPOGENIC COVARIATES

We hypothesized that giraffe home range sizes were correlated with covariates: (1) proportion of vegetation types in the home range; (2) distance of home range from human

settlements; (3) density of survey routes in the home range; (4) sex of the individual; and (5) local giraffe population density. We included giraffe population density (for estimation see below) as a factor because it is known to influence home range sizes of mammals (Kjellander et al., 2004; Schoepf et al., 2015).

We derived four vegetation types from a natural vegetation map developed by the University of Copenhagen's Vegetation and Climate Change in Eastern Africa (VECEA) project (downloaded from http://vegetationmap4africa.org/2_Vegetation_map.html). Representing closed to open habitats, categories included (1) deciduous bushland and thicket, (2) wooded grassland, (3) edaphic grassland on volcanic soils with scattered woody species and (4) edaphic grassland on drainage-impeded or seasonally flooded soils (Kindt et al., 2011). We mapped human-developed areas and bomas using Google Earth imagery. Bomas were small temporary family settlements built by members of the pastoralist Masai tribe that consisted of huts made of mud or cow dung, whereas developed areas were more densely populated towns with permanent concrete structures (Fig. 1).

We calculated local giraffe population density by dividing the number of adult giraffes by surveyed area (km^2) of each site, with surveyed area calculated as the minimum convex polygon enclosing the surveyed route network in each site, plus a boundary strip 500 m wide (Parmenter et al., 2003).

DATA ANALYSIS

Home range size—We estimated year-round home range sizes of adult (>3 years old) male and female giraffes by combining multiple years of relocations for each individual. Calves and subadult giraffes were not included in this analysis as natal dispersal may bias home range size, and home ranges of calves are not independent of the home range of their mothers. We applied

two different calculation methods to generate home ranges: the 100% minimum convex polygon (MCP) for comparison with previously published studies and the 95% utilization distribution (UD) with a kernel density estimator (Seaman & Powell, 1996) for testing predictions about home range correlates. Rather than drawing polygons around observed locations to create a minimum convex polygon, utilization distributions are density functions that describe the probability of an animal being present in an area (Jennrich & Turner, 1969). Börger et al. (2006) found the kernel method was the most unbiased home range estimator across sampling regimes and was robust to relatively smaller sample sizes, so we used this method to generate home ranges for our correlation analysis.

We employed a two-step process to estimate robust home range sizes by kernel density. For kernel density estimators, the choice of a smoothing parameter or bandwidth (h), can substantially affect results (Fieberg, 2007). If h is set too small, home ranges consists of patches around every location, but if h is set too large, then the home range border is placed far from the actual locations. First, to calculate the optimal bandwidth, we generated home ranges with a variety of h values and determined that $h = 1500$ provided the most reasonable configurations. We also generated home ranges with both 75% and 95% kernel utilization distributions (kernel UD). The 75% kernel UD excluded locations furthest from the core, which we believed underestimated the home range size. We therefore proceeded by using 95% kernel UD with $h = 1500$ for final analyses.

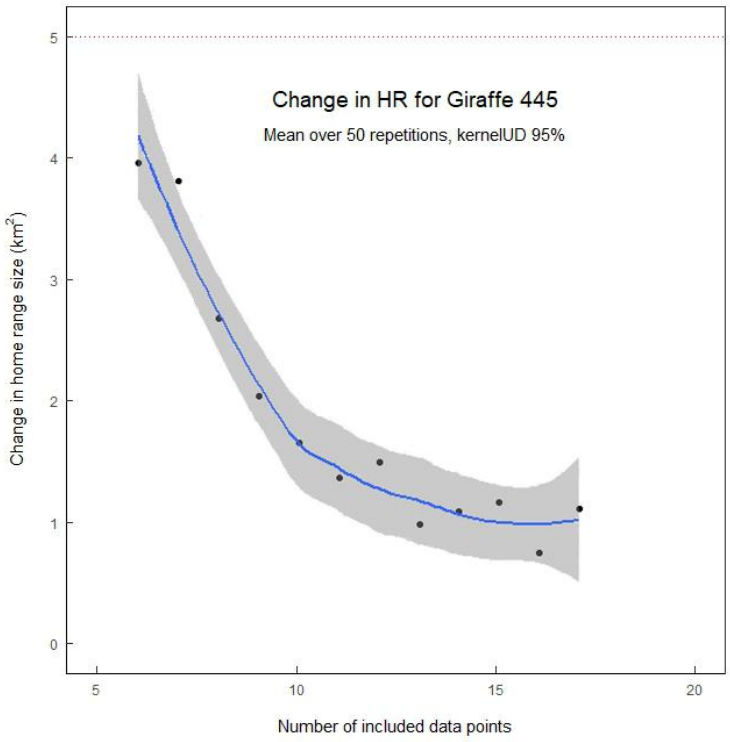

Figure 2. Example of stabilization of giraffe home range estimates with the bootstrap procedure.

Second, to determine whether an individual giraffe's 95% kernel UD home range estimate stabilized and was thus robust, we ran a bootstrapping algorithm in which, for each individual, we drew at random an increasing number of its relocation points and estimated the 95% kernel UD with each successive addition of a location (Tingley et al., 2014). We began by considering only adult giraffes with a minimum of 10 resights. We then generated home range estimates, starting with five randomly selected locations and successively integrating the remaining locations at random. We repeated the procedure 50 times per giraffe and calculated the mean change in home range size per added location. We inspected the graphs of change in home range size and considered the home range estimate to have stabilized when at least three successively added locations resulted in estimates with a <5 km change in area (e.g. Fig. 2). For the subsequent analysis of environmental and anthropogenic correlates of home range size, we used the subset of giraffes with stabilized home range estimates. We also added boundaries where the landscape acted as a barrier on giraffe movement for improved home range estimation and reduction of type II errors (Calenge, 2006; Fieberg & Börger, 2012). These barriers were the Lake Manyara shoreline, a rift wall in the western part of Lake Manyara National Park, and agricultural land between Tarangire National Park and Manyara Ranch

Conservancy (e.g. Fig. 3). We calculated all home range sizes using the package *adehabitatHR* (Calenge, 2006) in R (version 3.4.2).

HOME RANGE COVARIATES

In our analysis of ecological and anthropogenic correlates to home range size, we used only the subsample of giraffes residing in the northern part of Tarangire National Park and in Manyara Ranch Conservancy, because these areas had higher survey route coverage with respect to average giraffe home range size (Fig. 1). We were thus confident that our sample of giraffe home ranges did not extend significantly beyond our survey area. We also excluded giraffes living in Lake Manyara National Park because this park is relatively small, nearly isolated and contains little variation in vegetation.

We generated distances to human settlements by calculating the smallest distance from the edge of each individual's 100% MCP home range to both the nearest developed area and the nearest boma, using the function 'gDistance' in the R package *rgeos* (Bivand, 2018). We calculated the proportions of different vegetation types within each giraffe's 95% kernel UD home range (which included a larger area surrounding giraffe relocations than MCP, see Results) using the function 'intersect' in the R package *raster* (Hijmans & van Etten, 2012). The same procedure was conducted for survey route coverage, where kilometres of roads per area (km^2) were calculated for each 95% kernel UD home range with the 'intersect' function from R package *raster* (Hijmans & van Etten, 2012).

We used multiple linear regression and model selection to determine which variables best explained variation in log-transformed home range sizes of giraffes in our sample. Explanatory variables included sex, proportion of four vegetation types, distance from both bomas and towns, and local giraffe population density (see Table 2 for variables). We also tested models with

interactions between sex and giraffe population density, and sex and distance to towns. We developed and compared a suite of 14 a priori models reflecting various combinations of explanatory variables, including a null and global model. We used Akaike information criterion corrected for small sample sizes (AIC_c; Burnham & Anderson, 2002) and AIC weights (w_i) for model selection and model averaging. We considered models with $AIC_c < 2$ to be competitive, and we examined the degree to which 95% confidence intervals of the beta coefficients (ß) included 0 to determine the direction and precision of evidence for covariate effects. To account for model-selection uncertainty, we calculated model-averaged ß estimates and 95% confidence intervals by averaging from all weighted models and assuming ß = 0 for models in which an explanatory variable did not appear (Burnham & Anderson, 2002). We conducted model selection and averaging using the package *MuMIn* for R (Barton, 2018).

We collated mean home range estimates of adult male and female giraffes throughout the range of the species and obtained data on mean annual rainfall (mm) in each study area, from published sources. We conducted a simple linear regression analysis testing the effect of rainfall on mean log-transformed MCP home range sizes of both sexes combined. We used MCP because all but one of the previous studies estimated home range sizes using this method.

TABLE 1. **MEAN (+SD) HOME RANGE SIZES OF FEMALE AND MALE GIRAFFES, *GIRAFFA CAMELOPARDALIS*, METHODS, SAMPLE SIZES, GEOGRAPHICAL LOCATIONS (NP = NATIONAL PARK) AND MEAN ANNUAL PRECIPITATION FROM THIS STUDY AND REPORTED IN THE LITERATURE**

	Mean (SD) home range size (km^2)			Data collection method	Home range calculation method	Number of giraffes	Geographical location	Annual rainfall (mm)
	Females	Males	Both					
Masai giraffe, *G. c. tippelskirchi*								
	110.4 (54.9)	126.2 (67.9)	111.2 (55.3)	CMR[1]	95% Kernel UD	71	Tarangire NP, Manyara Ranch, Tanzania[2]	
	110.7 (24.6)	144.1 (27.4)	118.0 (28.4)	CMR	95% Kernel UD	37	Lake Manyara NP, Tanzania[2]	
	27.8 (23.2)	26.1 (17.6)	27.7 (22.8)	CMR	MCP 100%	71	Tarangire NP, Manyara Ranch, Tanzania[2]	650[12]
	12.5 (7.9)	19.8 (8.2)	14.0 (8.4)	CMR	MCP 100%	37	Lake Manyara NP, Tanzania[2]	915[13]
	9	5		CMR	Periphery method	~40	Lake Manyara NP, Tanzania[5]	
	85	62		CMR	MCP 100%	20	Nairobi NP, Kenya[3]	844[13]
	162	164	163	CMR	MCP 100%	110	Tsavo NP, Kenya[4]	553[13]
South African giraffe, *G. c. giraffa*								
	282			Radiocollar	MCP 100%	1	Kruger NP, South Africa[6]	312–650[13]
	177 (wet) 245 (dry)			Satellite GPS	MCP 95%	8	Khamab Kalahari Nature Reserve, South Africa[7]	333[7]
Angolan giraffe, *G. c. angolensis*								
	200	514		CMR and radiocollar	MCP 100%	60	Namib desert, Namibia[8]	13–100[8]
West African giraffe, *G. c. peralta*								

	50 (wet) 103 (dry)	32 (wet) 134 (dry)	CMR	MCP 100%	28 (wet) 17 (dry)	Sahel, Niger[9]	400–600[9]
Reticulated giraffe, *G. c. reticulata*							
	64	96	CMR	Kernel UD 75%	160	Ol Pejeta Conservancy, Kenya[10]	739[14]
Thornicroft's giraffe, *G. c. thornicrofti*							
	68	82	CMR	MCP 100%	27	South Luangwa NP, Zambia[11]	<500[15]

[1] Capture–mark recapture.
[2] This study.
[3] Foster and Dagg (1972).
[4] Leuthold and Leuthold (1978).
[5] van der Jeugd and Prins (2000).
[6] du Toit (1990).
[7] Deacon and Smit (2017).
[8] Fennessey (2009).
[9] Le Pendu and Ciofolo (1999).
[10] VanderWaal et al. (2014).
[11] Berry (1978).
[12] Foley and Faust (2010).
[13] Coe et al. (1976).
[14] Kavwele, Kimanzi, and Kinyanjui (2017).
[15] Bishop et al. (2016).

Results

We identified 1264 individual adult giraffes in the Tarangire-Manyara Ecosystem using photographic capture–mark–recapture methods. The bootstrapping procedure indicated that estimates of home range sizes stabilized for 132 giraffes (109 females and 23 males). We reported home range sizes for these individuals. Home range sizes of giraffes whose home range estimates stabilized did not differ significantly from home range sizes of giraffes whose estimates did not stabilize (Welch's two-sample *t* test: t_{245}= -1.25, P = 0.212), thus our sample was not biased towards individuals with smaller or larger home range sizes. Further subsetting of the data set by including only giraffes residing in Manyara Ranch Conservancy and northern Tarangire National Park resulted in a sample of 71 individuals (67 females and 4 males) that we used for testing correlates of home range size. The mean number of locations per giraffe in the final subset was 16.3 (SD = 3.06, range 10–24 locations).

Overall mean home range sizes (95% kernel UD, h = 1500) for giraffes in Tarangire and Lake Manyara National Parks and Manyara Ranch was 122.0 km^2 (SE = 50.8 km^2, N = 132), with a mean of 114.6 km^2 (SD = 49.0 km^2, N = 109) for females and 157.2 km^2 (SD = 44.9 km^2, N = 23) for males. Home range sizes of males were significantly larger than those of females (Welch's two-sample *t* test: t_{34} = -4.07, P < 0.0003). Mean 100% MCP home range sizes measured 24.1 km^2 (SD = 19.7 km^2), with a mean estimate of 23.3 km^2 (SD = 20.1 km^2) for females and 27.8 km^2 (SD = 17.7 km^2) for males, with no significant difference in size between males and females (t_{35} = -1.08, P = 0.288). The home ranges computed with minimum convex polygons were substantially smaller than with kernel density estimators, especially if resights occurred primarily along one survey route in a linear shape (e.g. Fig. 3). Table 1 reports site-specific home range sizes for 67 females and 4 males in Tarangire National Park and Manyara

Ranch Conservancy, and for 29 females and 8 males in Lake Manyara National Park, along with previously reported giraffe home range sizes throughout Africa from the literature.

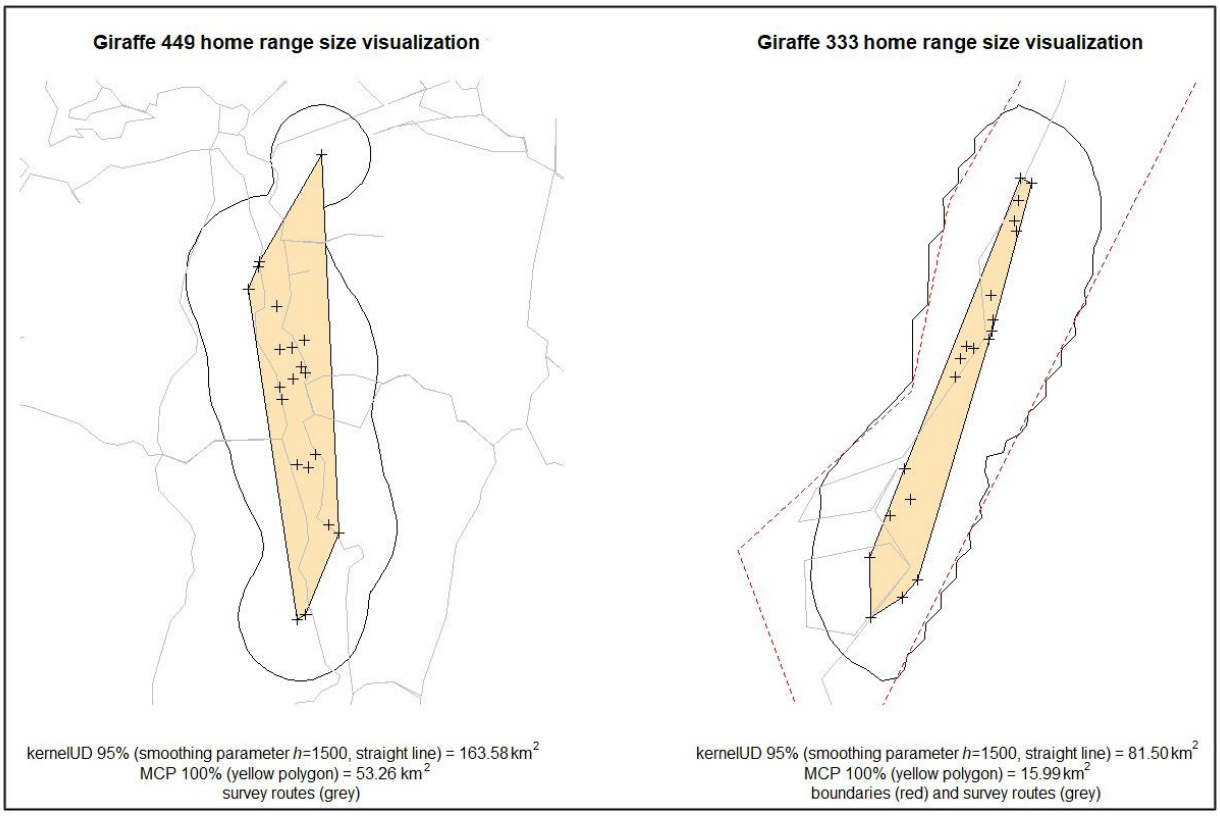

Figure 3. Visualizations of giraffe home ranges. Left: Male from Tarangire National Park. Right: Female from Lake Manyara National Park.

In our multiple linear regression analysis testing ecological and anthropogenic correlates of log-transformed home range size, regression diagnostics indicated that the dependent variable home range size was normally distributed and linearly related to the predictor values. Four models were competitive (<2 ΔAIC_c) and five models together carried 99% of weight (Table 2). The top-ranked linear regression model explaining variation in home range sizes of giraffes included developed areas (towns) ($P < 0.001$) and survey route density ($P = 0.051$), and this model carried more than twice the weight of the next-ranked model (Table 2). The predictors in the top model explained 19% of the variance in home ranges size ($R^2 = 0.191$, $P < 0.001$).

Model-averaged beta coefficients (Table 3) from all models carrying weight demonstrated a negative relationship between home range size and distance to towns (ß = -0.088, SE = 0.037, $P = 0.019$; Fig. 4), with no other significant explanatory variables.

Simple linear regression analysis of data from published studies throughout Africa indicated a significant negative correlation between mean annual rainfall in a study area and mean log of 100% MCP home range sizes of giraffes ($F_{1,8} = 26.25$, $P < 0.001$; Fig. 5). Regression diagnostics demonstrated that the dependent variable home range size was normally distributed and linearly related to the explanatory variable rainfall. This relationship explained a large proportion of variation in home range sizes throughout the range of the species ($R^2 = 0.74$).

Table 2. Model selection results from 14 linear regression models showing top-ranked five models explaining variation in 95% kernel utilization distribution home range sizes of 71 giraffes (67 females and 4 males) in the Tarangire-Manyara Ecosystem, based on maximum likelihood estimation

Model	Intercept	Bomas[1]	Towns[2]	PopDen[3]	Survey routes[4]	Sex	Veg1[5]	Veg2[6]	Veg3[7]	Veg4[8]	PopDen *sex	Towns *sex	*K*	AIC_c	ΔAIC_c	w_i
m 3	5.34	—	-0.08	—	-0.83	—	—	—	—	—	—	—	3	108.46	0.00	0.44
m 12	4.92	—	-0.11	—	—	—	—	—	—	—	—	—	2	110.21	1.75	0.18
m 1	5.83	-0.06	-0.10	-0.20	-0.90	0.30	—	—	—	—	—	—	6	110.36	1.91	0.17
m 11	4.86	—	-0.10	—	—	1.06	—	—	—	—	—	-0.17	4	110.43	1.97	0.16
m 7	5.36	—	—	—	-1.29	—	—	—	—	—	—	—	2	113.24	4.78	0.04

Models shown here are those that carried 99% weight. ΔAIC_c is the difference in AIC_c values between a model and the top-ranked model. *K* is the number of parameters in a model. w_i is model AIC_c weight, a metric for strength of evidence supporting a given model as the best description of the data.

[1] Distance (km) from edge of 100% MCP (minimum convex polygon) home range to nearest boma.

[2] Distance (km) from edge of 100% MCP home range to nearest town.

[3] Local giraffe population density.

[4] Density (km) survey routes in 95% kernel utilization distribution.

[5] Proportion Veg1 (*Acacia–Commiphora* deciduous bush-land and thicket) in 95% kernel utilization distribution.

[6] Proportion Veg2 (edaphic grassland on drainage-impeded or seasonally flooded soils) in 95% kernel utilization distribution.

[7] Proportion Veg 3 (edaphic grassland on volcanic soils with scattered woody species) in 95% kernel utilization distribution.

[8] Proportion Veg4 (*Acacia–Commiphora–Combretum* wooded grassland) in 95% kernel utilization distribution.

Table 3. Model-averaged parameter estimates, standard errors, 95% confidence intervals and *P* values from multiple linear regression models explaining variation in home range size of 71 giraffes in the Tarangire-Manyara Ecosystem of northern Tanzania.

Parameter	Estimate	SE	95% CI	*P*
(Intercept)	5.27	0.41	4.47 to 6.07	0.000
Routes	-0.57	0.54	-1.73 to -0.02	0.296
Towns	-0.09	0.04	-0.16 to -0.03	**0.019**
PopDen	-0.03	0.10	-0.54 to 0.13	0.740
Sex (M)	0.22	0.45	-0.42 to 1.77	0.620
Bomas	-0.01	0.05	-0.26 to 0.15	0.842
Towns*sex	-0.03	0.07	-0.36 to 0.02	0.706

Averages assume a variable is included in every model but in some models the corresponding coefficient and its variance is set to zero. Significant *P* values are shown in bold.

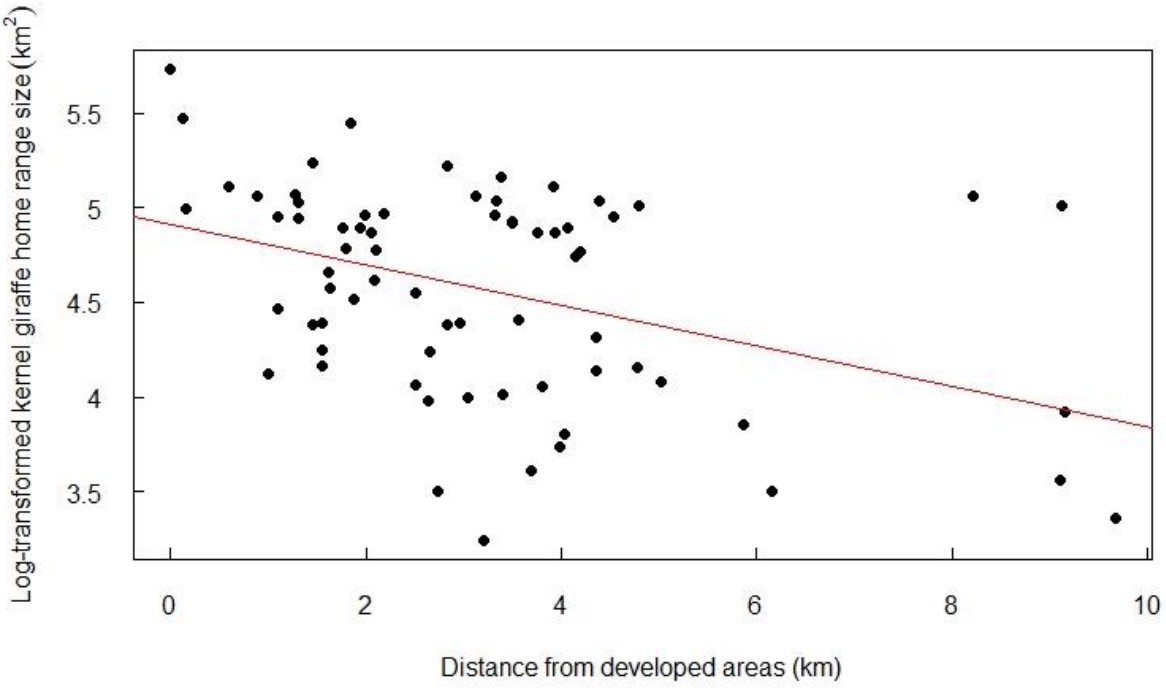

Figure 4. Log-transformed kernel home range sizes (km^2) of giraffes in the Tarangire-Manyara Ecosystem as a function of distance from developed areas (km).

Discussion

We found that home range sizes of adult female Masai giraffes at an ecosystem scale

were significantly larger in areas closer to towns with high densities of humans compared with surrounding landscapes. Vegetation type, local giraffe population densities and distance to traditional pastoralist family compounds (bomas) had no significant influence on space use by giraffes in our study area. Throughout Africa, home range sizes of adult giraffes significantly decreased with increasing mean annual rainfall.

ECOLOGICAL AND ANTHROPOGENIC CORRELATES OF HOME RANGE SIZE

Our analysis of anthropogenic and ecological correlates of individual home range sizes in the Tarangire-Manyara Ecosystem indicated that use of space by giraffes was influenced primarily by the individual's proximity to densely populated towns (Fig. 4). The farther from developed human areas, the smaller the giraffe home range size—but no such correlation was evident with bomas, which are dispersed family homesteads built by members of the pastoralist Masai tribe. Contrary to our predictions based on determinants of home range sizes for other ungulate species, home range sizes of giraffes were not significantly correlated with vegetation type or local giraffe population density. Kjellander et al. (2004) hypothesized that conspecifics will compete for local resources and thus limit each other's use of space when densities are high, resulting in smaller individual home ranges. However, we did not observe this in our study.

As expected, giraffes living closer to densely populated towns had significantly larger home range sizes, indicating a need to travel greater distances to obtain critical resources while avoiding human disturbance. Kie et al. (2002) noted that in landscapes where habitats are less interspersed, large herbivores must travel longer distances to the nearest patches of suitable habitat once forage is depleted or because of anthropogenic disturbance (including human predation risk). This increased expenditure of energy might play a role in the lower survival and population growth rates of giraffes observed outside protected national parks in this study area

(Lee & Bolger, 2017; Lee et al., 2016). Indeed, habitat fragmentation caused by logging was correlated with larger home range sizes and subsequent reduced fitness of spotted owls, *Strix occidentalis*, in forests of the western United States (Carey et al., 1990; Glenn et al., 2004); thus, patterns of home range size may offer proxy measures for evaluating habitat quality. Giraffe habitat tends to be degraded or lost near dense areas of human habitation, as people often cut trees for fuelwood and much of the landscape surrounding towns has been converted to agriculture. However, no such negative relationship with home range size was observed with distance to bomas, suggesting either that traditional land uses as practiced by nomadic pastoralists do not adversely affect use of space by adult female giraffes, or that space use by giraffes is a function of human population density. Anthropogenic disturbances leading to habitat loss and fragmentation are among the biggest threats to global biodiversity (Lindenmayer & Fischer, 2013). Land-use planning and zoning that takes into consideration the needs of large herbivores can help sustain populations in increasingly human-dominated landscapes (Lee, 2018; Lee & Bond, 2018).

The 95% kernel UD (utilization distribution) home ranges of 23 males were significantly larger than ranges of 109 females in the entire Tarangire-Manyara study area. This result is similar to the only other study of giraffe home ranges to utilize kernel estimators, for reticulated giraffes, *G. c. reticulata*, in Kenya (VanderWaal et al., 2014). Adult male giraffe life-history strategy is to roam among female herds in search of females in oestrus (Dagg, 2014). Interestingly, no such sex differences in home range sizes were evident using MCP (minimum convex polygon) methods in our study and in most other studies of giraffes, with the exception of populations in Namibia and Zambia (Table 1), providing further evidence that MCP methods may be less accurate than kernel estimators (Börger et al., 2006). Sex was not a significant

predictor of home range size in our linear models, but this is likely due to the small sample size of adult males who had robust, stabilized home range estimates (N = 4). Thus, our inference about correlates of home range size at the ecosystem scale should extend to adult females only.

Börger et al. (2006) demonstrated that most variation in home range size within a study population is due to differences between individuals, regardless of the estimation method used, and recommended increasing the number of individuals tracked at the expense of obtaining more locations per individual. The relatively large sample of 132 individual giraffes whose 95% kernel UD estimates stabilized suggests that our methods and data were appropriate for testing general patterns of home range sizes in our study area. Individuals whose home range sizes stabilized over the study period might nevertheless differ in other aspects of their behaviour from those of the remaining population, by being more dominant during access to food or being more sedentary.

AFRICA-WIDE HOME RANGE COMPARISONS

Home range sizes of giraffes in the Tarangire-Manyara study area were generally smaller than in other regions of Africa, although home range estimates among studies were highly variable (Table 1). One potential factor driving variation in home range size among study populations across the African continent could be differences in rainfall and the availability of surface water (Deacon & Smit, 2017). We found that mean annual rainfall in a study area explained 74% of the variation in mean MCP home range size of giraffes. The smallest recorded giraffe home range sizes were in Lake Manyara National Park, and annual precipitation was relatively higher in Lake Manyara National Park than in all the other study areas (Table 1). In the most arid study area, the Namib desert, giraffe home range sizes reached up to 1900 km^2 (giraffe bull), which may be correlated with low forage density, increased searching for females and low

giraffe population density (Fennessy, 2009).

The relationship we documented between rainfall and space use by a large herbivore is not surprising, given that rainfall mediates primary productivity (food resource availability) which in turn mediates space use by ungulates (McNaughton, 1985; McNaughton et al., 1988). The negative correlation we observed between space use by giraffes and rainfall—and therefore productivity—at the continent-wide scale reflects a similar pattern as that of home range size and distance from towns at the ecosystem scale: the greater the availability and access to critical resources such as food and water, the smaller the home range. Human disturbance and fragmentation of habitat in and around densely populated areas likely reduced the local forage and water resources available for giraffes, forcing individuals to increase their movements and use of space to obtain these resources. Similarly, lower primary productivity forces individuals to range more widely (Fennessey, 2009).

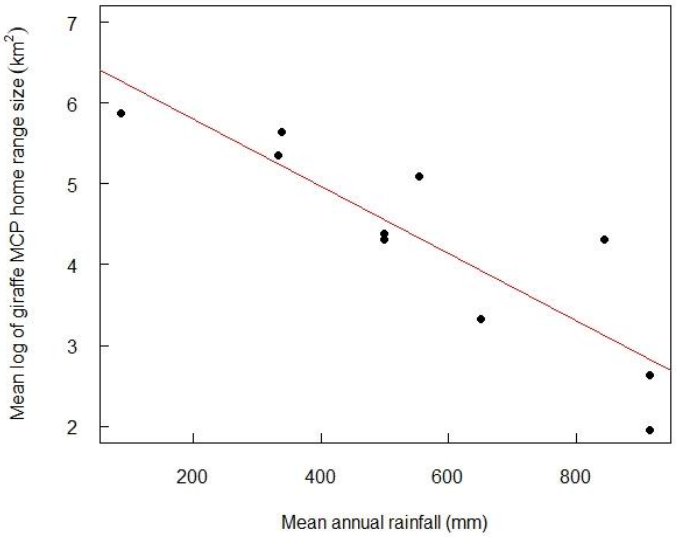

Figure 5. Log-transformed minimum convex polygon (MCP) home range sizes (km^2) of giraffes as a function of annual rainfall (mm) from 10 study areas throughout Africa.

MCP VERSUS KERNEL ESTIMATORS

Most previous published estimates of giraffe home range sizes used minimum convex polygon methods to calculate area (Table 1). Unfortunately, the MCP method has been found to be highly inefficient and biased, especially for small sample sizes of individuals and relocations

(Börger et al., 2006). Minimum convex polygons provide only crude outlines of the range, are sensitive to extreme data points ("occasional sallies" as defined by Burt, 1943), fail to take into account information provided by the interior locations and approach asymptotic values of home range area only with large samples sizes (Powell, 2000). Whether to calculate home range sizes with minimum convex polygons or kernel utilization distribution depends on how the data were collected and on the research question (Börger et al., 2006; Fieberg & Börger, 2012). In our case, if surveys are conducted less frequently, there is a greater probability of missing detections at the edge of the range. Using MCP calculations could then lead to underestimation of the home ranges, which may underlie the much smaller MCP estimations in our study and others that compared MCP with kernel estimates using the same data (e.g. ocelots, *Leopardus pardalis*: Dillon & Kelly, 2008; African buffalo, *Syncerus caffer*: Ryan et al., 2006). MCP methods also failed to differentiate between larger home range sizes of males than females that were observed with kernel density estimates (Dillon & Kelly, 2008). For smaller sample sizes the kernel UD is likelier more robust. Nevertheless, for both methods a minimum number of data points per individual is needed to obtain an accurate estimation of the home range size (Börger et al., 2006). Therefore, we suggest utilizing home range estimates from individuals with a minimum number of relocations required for unbiased estimation, either by using a bootstrap procedure or another method, and when possible consider using kernel density estimators while taking into account barriers to movement.

CONCLUSIONS

Our study supports the hypothesis that home range sizes of large herbivores vary with access to or availability of resources. Furthermore, access or availability was influenced by anthropogenic factors. We found that 10% of the adult giraffes analyzed had stable home range

sizes over a period of 6 years, and that those stable home ranges did not differ significantly in size from those of the remainder of the population. This may suggest that giraffes, instead of modifying the size of their home range, may move to areas of better suitability, a phenomenon that we did not address here. Nevertheless, in areas characterized by intensive human disturbance (but not in traditional pastoralist areas), adult female giraffes consistently roamed over larger areas at the landscape scale. At the continent-wide scale, primary productivity as indexed by rainfall mediated home range sizes of adult giraffes. Our results should help wildlife managers make informed decisions that improve conservation plans for at-risk species such as giraffes.

Conclusion

All animal populations exhibit some degree of sociality, ranging from mostly solitary to highly gregarious, and individuals can either associate randomly or form preferred and avoided relationships, giving rise to social structure in a population (Alexander 1974, Whitehead 2008b). Additionally, the same individuals under varying ecological circumstances can switch from being solitary to being social, suggesting adaptive social flexibility (Schradin et al. 2012). Understanding how and why individual social behaviors and social structure of populations vary in different habitats and with different degrees of human influence can reveal potential ecological and anthropogenic drivers of sociality (Leu et al. 2016, Maldonado-Chaparro et al. 2018). Further, examining fitness consequences of sociality and sociability in a diverse socioecological landscape can provide insights into the evolution of social systems (Silk et al. 2009; 2010). The socioecological landscape is the environment in which natural selection occurs, and socioecology is the framework for understanding grouping dynamics, social relationships, and dispersal tendencies as adaptive responses to elements of the social and ecological environment. In this PhD I sought to understand how the socioecological environment mediates sociality and fitness, namely fission-fusion dynamics of groups, social structure, survival and reproduction, natal dispersal, and space use, in a large tropical herbivore with a highly fission-fusion social system, the giraffe.

I investigated factors underlying social and spatial population structure in a large metapopulation comprising thousands of giraffes by integrating: (1) features of local ecological environment for each individual and social community, including vegetation structure and preferred plant forage species as well as distance to both traditional (bomas) and modern human settlements (towns); (2) social behavior as represented by the number, strength, and exclusivity

of relationships as well as movements among groups; (3) demographic rates of survival and reproduction; and (4) spatial and social movements of young giraffes as they aged from calf to subadult. I selected the ecologically heterogeneous Tarangire Ecosystem in northern Tanzania as my study area because it is a coupled human-natural landscape with a rapidly growing human population surrounding several protected areas, which enabled me to explore the effects not only of natural predation and vegetation, but proximity to varying levels of human presence, and to elucidate the potential differences between traditional pastoralist lifestyles versus modern human development with its concomitant poaching and habitat conversion, on sociality and demography of giraffes. This information is particularly important as human pressures on wildlife are projected to increase in what has been termed the Anthropocene Era (Ceballos et al. 2017).

I used the same suite of ecological and social covariates in several different but complementary analyses to build a narrative of giraffe sociality and fitness in a landscape facing ever-increasing human pressures, similar to pressures faced by wildlife species across the globe. I focused on the giraffe metapopulation that spans 4,400 km^2 in the heart of the ~30,000 km^2 Tarangire Ecosystem (Lee et al. 2016a). With two world-class national parks, two adjacent Wildlife Management Areas, and a ranch conservancy, within a matrix of unprotected village lands—all unfenced and connected by giraffe movements—the study area incorporates the majority of giraffes in the entire ecosystem (Tanzanian Wildlife Research Institute aerial data). In my multi-year photographic capture-recapture study of more than 3,000 uniquely identified individuals, I found that grouping patterns of giraffes were influenced by food availability, predation risk, and presence of humans, with particular requirements for mothers with calves (chapter 1). Using social network analysis, I parsed the metapopulation into 14 distinct, modular communities of socially associated adult female giraffes, with 11 communities large enough to

test hypotheses explaining variation in social structure (chapter 2). Adult females in communities closer to traditional human settlements called bomas had weaker relationship strengths among all members of the community and more exclusive relationships with fewer other females, suggesting that the presence of humans disrupted their social structure. Most of the giraffe social communities overlapped in space, with several overlapping substantially, allowing me to explore social versus ecological drivers of variation in reproduction and survival among 10 of the communities with sufficient numbers of adult females and calves for demographic analysis (chapter 3). Community-level demographic rates were correlated with vegetation and proximity to humans, as communities with more dense bushlands had lower calf survival while those closer to human settlements had higher reproductive rates. Adult female survival did not differ among communities, but in chapter 4 I reveal that more gregarious females (being in larger groups) and females that associated with more groups had higher survival. I propose that survival of adult female giraffes is improved by being well-integrated into their larger social community through having many weaker bonds rather than by forming stronger and highly stable bonds with just a few individuals. This result implies that the disruption of social structure as evidenced in chapter 2, with females forming more exclusive relationships with fewer individuals and weaker relationships with the others in their community could have demographic consequences, although proximity to bomas did not influence adult female survival as much as their level of sociability (chapter 4). Overlapping social communities also enabled me to investigate social versus spatial natal dispersal by subadult giraffes in chapter 5. I found that young females rarely dispersed, and social dispersal was even more infrequent, again confirming the importance that females place in maintaining social ties with other females from calf to adulthood. Conversely, most young males dispersed, both socially and spatially. Previous research in Namibia

documented that female giraffes with preferred relationships were more genetically related than expected (Carter et al. 2013a), thus the social communities of more strongly associated individuals in our study area likely comprise related females. Natal dispersal of males into new social communities that were close to their natal area suggests they may be able to seek a new pool of unrelated females with whom to mate, without the need to travel long distances into unfamiliar areas. Calves born in communities closer to towns were less likely to socially-and-spatially disperse, and calves born in communities with higher local giraffe population densities—several of which were relatively closer to towns, but also situated in areas with nutrient-rich volcanic soils— were less likely to spatially disperse. This result suggests that spatial variation in habitat quality might influence where giraffes congregate, which might in turn influence dispersal decisions and distances moved. Finally, human presence also influenced adult space use, as adult females living closer to densely populated towns had significantly larger home ranges, but no such relationship was evident with bomas, indicating a difference in anthropogenic impact between traditional versus modern human lifestyles on movements of giraffes (chapter 6).

This research is the first ever to model ecological and social covariates to social structure and space use, to compare ecological versus social influences on fitness, and to quantify patterns of natal dispersal of this iconic megaherbivore. I highlight and summarize several key findings in this conclusion. First, building upon previous social network research on reticulated giraffes in Kenya that showed clusters of cliques embedded in subcommunities that were themselves embedded in two spatially separated communities (VanderWaal et al. 2014), I uncover an additional level of social organization, that of many distinct, overlapping communities each comprised of ~60–90 adult females within a larger-scale metapopulation (chapter 2). This

analysis was made possible by my large sample size (>500 adult females seen ≥6 times) within a vast, contiguous unfenced landscape. I then showed that these overlapping social communities exhibited different demographic rates that could be attributed to ecological and anthropogenic factors (chapter 3). Further, natal dispersal of young male giraffes, but not young females, into nearby social communites indicates that males may view their new community as a pool of unrelated females with whom to mate (chapter 5). Thus, the use of social associations to define subpopulations (communities) for demography and dispersal movements elucidated a new level of biologically meaningful population structure for giraffes. Previous demographic analyses in my study metapopulation compared vital rates of giraffes in five spatially separated administrative areas (Lee et al. 2016a), so the greater number of divisions (≥ 10) created by social network analyses enabled finer-scaled investigation of environmental and social covariates across the landscape that highlighted specific subpopulations (i.e. communities) which had greater or lesser fitness, even within the same administrative area.

Second, I discovered a complex, mixed relationship between people and giraffes. Disturbances around towns likely represents a threat, as adult females inhabiting areas close to towns had to range more widely (chapter 6), and mothers with calves were less likely to be found in places close to towns (chapter 1). Additionally, relationships among females in communities closer to bomas exhibited signs of repeated social disruption (chapter 2), suggesting impacts on social relationships of giraffes not only from modern human development but also traditional human pastoralists with their livestock. On the other hand, giraffe mothers appeared to seek out areas closer to bomas to protect their calves from natural predators such as lions and hyenas, as reflected in the higher likelihood of finding calf groups near bomas (chapter 1) and the higher reproductive rates of communities nearer to bomas (chapter 3). Bomas also did not influence

natal dispersal probabilites or distances moved by young giraffes (Chapter 5). Further, adult females did not have larger home ranges around bomas as they did around towns (chapter 6), so the presence of traditional human pastoralists does not appear burden these females with additional energetic costs in terms of space use. Areas near bomas in the Tarangire Ecosystem have artificially low predation levels (Lichtenfeld 2005), which may attract giraffe mothers despite the disruption to their social relationships. Overall, I propose that female giraffes face a trade-off between maintaining social bonds within their community and reducing predation risk to their calves, and while bomas appear to be compatible with the persistence of giraffe populations, care must be taken to reduce potential adverse impacts such as disruption to their social structure. Towns represent a greater threat to giraffes and I recommend reducing disturbance around densely population human settlements, such as curbing poaching and agricultural expansion, to help recover and stabilize giraffe populations in the Tarangire Ecosystem and elsewhere in their range.

Third, I elucidated the importance of social relationships to survival of adult female giraffes. The link between social ties and fitness has been well-established in humans (House et al. 1998) and other primates (Alberts 2019) as well as in other taxa with highly intricate social systems and complex cognitive abilities such as dolphins (Frère et al. 2010), and even bighorn sheep (Vander Wal et al. 2015). My research further confirms a connection between greater sociability and survival in yet another high fission-fusion species. I documented substantial individual variation in social behaviours of adult female giraffes, and showed that those who roamed in groups with at least three and up to about nine other females, and associated more often with different groups, increased their survival probabilities. Their social relationships with other females are not particularly strong or stable in the short term, but they maintain bonds over

the long term (Bercovitch and Berry 2013, Carter et al. 2013b). Further, young females rarely dispersed socially, providing additional evidence that long-term bonds with many other community members is a feature of female giraffe societies. I found that the establishment of many social bonds within their larger community was more important to their survival than ecological and anthropogenic factors. Females may be using social cues to seek out and join with an optimal number of other females to obtain high-quality food, reduce stress levels, or experience physiological benefits of being around familiar 'friends.' As longevity is the most important determinant of female lifetime reproductive success in giraffes (Bercovitch and Berry 2016), more sociable phenotypes likely have enhanced fitness.

Understanding the drivers and fitness consequences of variation in socialty in a population as well as variation in individual sociability, and how these social traits are related to the natural environment as well as anthropogenic factors, is critical for developing effective conservation strategies in the Anthropocene. Translocations, for example, are increasingly used as a tool to re-introduce giraffes into areas where they have been extirpated or to establish populations in new areas (Lee et al. 2020). However, the importance of social relationships among females from calf to adulthood that I have demonstrated here suggests that disrupting those relationships through translocations could have long-term survival consequences, and the the need for capture and translocation of giraffes should be carefully considered. Further, quantifying the effects of traditional versus modern human lifestyles on giraffe social relationships and fitness can help predict the effects of human population expansion into giraffe habitats, and can provide guidance for land-use planning that successfully conserves giraffes.

Investigating potential links among the physical environment, sociality, and demography requires long-term, large-scale studies, because such studies are more likely to include

contrasting ecological and social conditions (Clutton-Brock and Sheldon, 2010). These types of studies provide invaluable data to examine many potential drivers of fitness in natural landscapes, including social (e.g., relationship strength and exclusivity, movement among groups), spatial (e.g., vegetation, natural predation, human presence), temporal (e.g., season, climate), and individual-based factors (i.e. age, disease status, spot pattern, body condition). I am fortunate that nearly a decade ago I helped establish and continue to participate in an ongoing, longitudinal demography study of thousands of uniquely identified giraffes in a vast coupled human-natural ecosystem, and my hope is that this project can continue to explore and learn what helps this megaherbivore to survive and thrive into the future.

Appendix

```
#################################################################################################
### R code for Chapter 1: “Fission-fusion dynamics of a megaherbivore are driven by ecological,
### anthropogenic, temporal, and social factors.”
### MONICA L. BOND ET AL. UNIVERSITY OF ZURICH
#################################################################################################

library(MCMCglmm)

#  GROUP SIZE AS RESPONSE
#  Model group size with generalized linear mixed models using zero-truncated Poisson distribution
#  Random effect of group

prior1 <- list(R=list(V=1,fix=1),
          G=list(G1=list(V=1, nu=1, alpha.mu=0, alpha.V=1000)))

GrpSize <- MCMCglmm(NumInd ~ POPDEN + LION + shortr + dry + hour + hour2 +
                  asin(P_AM) + asin(P_C) + D_Boma + D.Town + GENVEG +
                  SPVEG + SPVEG:dry + SPVEG:shortr + GENVEG:hour +
                  dry:LION + shortr:LION + SPVEG:LION + + GENVEG:LION
                 + asin(P_C):SPVEG + asin(P_C):GENVEG + GENVEG:asin(P_C):dry +
                  GENVEG:asin(P_C):shortr + GENVEG:asin(P_C):LION,
                random = ~GrpNum,
                family="ztpoisson", prior = prior1, pr = FALSE, pl = FALSE, verbose = FALSE,
                nitt=100000,burnin=5000,thin=100, data=data)

summary(GrpSize)
plot(GrpSize$Sol)
plot(GrpSize$VCV)

#  GROUP COMPOSITION: TYPE (BACH, SM, SF, MIXED, CALF) AS RESPONSE
#  Model group composition with generalized linear mixed models using multinomial logit distribution
#  Random effect of group

# One parameterizes a multinomial model as series of binomial contrasts (level 1 vs level 2, level 1 vs
# level 3) and fits a series of models. This is actually a complete model because any two-category subset
# of a multinomial model is conditionally binomial (i.e. if you know it’s A or B, then A is a binomial
# sample from (A+B)); any complete set of pairs is a valid parameterization.
# Units is the response variable value, and trait is the response variable name, which corresponds
# to the categories. By specifying rcov = ~us(trait):units, you are allowing the residual variance
# to be heterogeneous across "traits" (response categories) so that all elements of the residual
# variance-covariance matrix will be estimated.

## k = number of categories in response variable
k <- length(levels(data$TYPE))
## I and J are matrices that will set up constraints on the residuals of the model
I <- diag(k-1)
```

```
J <- matrix(rep(1, (k-1)^2), c(k-1, k-1))
## set up prior. The R-structure is the variance-covariance matrix for the residuals.
# the G-structure is the variance-covariance matrix for the random effects. The R-structure
# in this case is set to have a fixed-form (fix=1). For data where each observation is a single
# sample from a distribution over k categorical outcomes, we cannot estimate the residual
# variance because it depends on the mean-fixing the variance to be 1 for all the diagonal terms
# (variances)
prior1 <- list(R = list(fix=1, V = (1/k)*(I + J), n = k),
          G=list(G1=list(V=diag(k-1), n = k)))

# In the model we say trait-1 to guarantee an intercept for each non-baseline level of
# the outcome, rather than an overall intercept term with an offset for k-2 levels
# Right of the colon is the grouping variable. rcov is the structure of the residuals (units
# refers to each individual observation, and this specification of the variance-covariance
# matrix of the residuals allows arbitrary correlations in the errors). We use "categorical"
# distribution because we have data that consists of one line per observation.

GrpComp <- MCMCglmm(TYPE ~ -1 + trait*D_Boma - D_Boma + trait*SPVEG - SPVEG  +
                    trait*GENVEG - GENVEG + trait*D.Town - D.Town + trait*SEASON - SEASON +
                    trait*SEASON:SPVEG,
                random = ~us(trait):GrpNum,rcov = ~us(trait):units,
                prior=prior1, family="categorical", pr = FALSE, pl = FALSE, verbose = FALSE,
                nitt=100000,burnin=5000,thin=100, data=data)
summary(GrpComp)
plot(GrCmp$Sol)
plot(GrCmp$VCV)

#  GROUP COMPOSITION: PROPORTION CALVES AS RESPONSE
#  Generalized linear mixed models with the binomial distribution
#  Random effect of group

prior1=list(R=list(V=1, nu=0.002), G=list(G1=list(V=1, nu=0.002)))

PropCalves<-MCMCglmm(cbind(C, NumInd) ~ LION + shortr + dry + D_Boma + D.Town + GENVEG
                    + SPVEG + dry:GENVEG + shortr:GENVEG + GENVEG:LION + dry:LION +
                    shortr:LION,
                random = ~ GrpNum,
                family = "multinomial2",
                data = data, verbose = FALSE,
                nitt=100000,burnin=5000,thin=100,
                prior=prior1)
summary(PropCalves)
plot(PropCalves$Sol)
plot(PropCalves$VCV)
```

```
##############################################################################################
### R code for Chapter 2: “Proximity to humans affects local social structure in a giraffe metapopulation”
### MONICA BOND ET AL UNIVERSITY OF ZURICH
##############################################################################################

##############################################################################################
#  1.  Begin social network analysis
##############################################################################################

# Load required libraries
library(asnipe)

#get group by individual matrix using asnipe
giraffe_gbi <- get_group_by_individual(giraffe, data_format = c(“individuals”))
head(giraffe_gbi[,1:10])

###get network using asnipe
giraffe_network <- get_network(giraffe_gbi, data_format = "GBI", association_index = "SRI")
diag(giraffe_network) <- 0

mean(giraffe_network) # tells us mean edge weights
sd(giraffe_network)
mean(giraffe_network>0) # mean non-zero edge weights
sd(giraffe_network>0)

##############################################################################################
#  2. Check if the networks are more structured than expected by chance/preferred avoided relationships
#  *permutation* of edge weights; report slope of coefficient of edge weight, CV of edge weights, and p-
# value. Restrict swaps to individuals seen in the same sampling event and the same management unit
##############################################################################################

#start by making a function to calculate coefficient of variation
cv <- function(x) {
  return (sd(x)/mean(x))
}

#let's calculate cv of observed data
observed <- cv(giraffe_network)
observed

#define a new variable, make permutations equal to 1000
permutations <- 10000

#generate random networks contricting within sampling occasion and site
networks.random <- network_permutation(association_data=giraffe_gbi,
                                       data_format = "GBI",  permutations=permutations, returns=1, association_index
                                       = "SRI",
```

```
                    association_matrix=giraffe_network, days=g_occ, within_day=TRUE,
                    locations=g_site,
                    within_location=TRUE
                    )

#calculate CV values for each random network. First we need to create a loop, repeating NA 1000 times,
random <- rep(NA, permutations)
for (i in 1:permutations) {
  random[i] <- cv(networks.random[i,1:540,1:540]) ## I have 540 females in my sample
}

observed
random
mean(random)

#plot observed vs random
par(mfrow=c(1,1))
hist(random, breaks=1000, xlab="CV of edge weights from randomized networks", main="",
xlim=c(3.8,5.0))  # specific to your data
abline(v=observed, col="red")
#the p-value is the number of times the CV value of the observed network is smaller than a
#randomized network, divided by the number of randomizations
sum(abs(observed) < abs(random))/1000

##############################################################################################
#  3. Run 4 community detection algorithms on 3 datasets; examine modularity Qs
##############################################################################################

# Load required libraries
library(igraph)

#convert adjacency matrix to igraph variable
giraffe_net <- graph.adjacency(giraffe_network, mode="undirected",diag=FALSE, weighted=TRUE)
plot(giraffe_net)

### community detection with cluster-walktrap as an example
cw <- cluster_walktrap(as.undirected(giraffe_net))
length(cw)
modularity(cw)
membership(cw)

### Randomize networks and get modularity of randomized networks
cw <- function(x) {
  igraph.obj <- graph.adjacency(x, mode="undirected",diag=FALSE, weighted=TRUE)
  random.cw <- cluster_walktrap(as.undirected(igraph.obj))
  random.mod <- modularity(random.cw)
  return (random.mod)
}
```

```
permutations <- 1000
networks.random.cw <- network_permutation(association_data=giraffe_gbi, data_format = "GBI",
                                permutations=permutations, returns=1, association_index = "SRI",
association_matrix=giraffe_network,
                                days=g_occ, within_day=TRUE, locations=g_site, within_location=TRUE)
random_cw <- rep(NA, permutations)
for (i in 1:permutations) {
  random_cw[i] <- cw(networks.random.cw[i,1:540,1:540])
}

# q observed
cw <- cluster_walktrap(as.undirected(giraffe_net))
plot(cw, as.undirected(giraffe_net))
length(cw)
qobs <- modularity(cw)
qobs
# q random
qrand <- mean(random_cw)
qrand
#the p-value is the number of times the modQ value of the observed network is smaller than a
#randomized network, divided by the number of randomizations
sum(abs(qobs) < abs(random_cw))/1000
par(mfrow=c(1,1))
hist(random_cw)
hist(random_cw, breaks=100, xlab="Cluster-walktrap modularity Q from random networks", main="")
par(xpd=FALSE)
abline(v=qobs, col="red")

##############################################################################################
#   4. Run community assortativity to test robustness of community assignments
##############################################################################################

# Load required libraries
library(igraph)
library(asnipe)
library(assortnet)

#load & check dataset. This will print the first 10 rows of the data, called 'gbi'
head(giraffe_gbi)

#Function to calculate rc, with default number of bootstraps = 100, and default option to plot result.
n.bootstraps <- 1000

calc_rc=function(giraffe_gbi, n.bootstraps=n.bootstraps, plot.result=F){

  # Create space to store results from bootstraps
  network.community <- matrix(0,ncol(giraffe_gbi),ncol(giraffe_gbi))
  network.present <- matrix(0,ncol(giraffe_gbi),ncol(giraffe_gbi))

  # 1. Calculate network
  network <- get_network(giraffe_gbi,data_format="GBI", association_index="SRI")
```

```
  # 2. Calculate community membership of the observed network
  community.observed <-
cluster_walktrap(graph.adjacency(network,mode="undirected",weighted=TRUE))
  community.observed

  # 3. Main bootstrapping method: i) Bootstrap the observed data, ii) recalculate the network,
  #    iii) recalculate community membership, iv) check if both individuals are observed

  for (i in 1:n.bootstraps) {
    # This step bootstraps the sampling periods
    gbi.boot <- giraffe_gbi[sample(1:nrow(giraffe_gbi),nrow(giraffe_gbi),replace=TRUE),]
    network.boot <- get_network(gbi.boot,data_format="GBI", association_index="SRI")

    # This step calculates the community membership from the bootstrapped network
    community.boot <-
cluster_walktrap(graph.adjacency(network.boot,mode="undirected",weighted=TRUE))

    # This step adds 1 to any dyads in the same community
    network.community <- network.community + outer(community.boot$membership,
community.boot$membership,"==")

    # This step adds 1 to any dyads that are both present (in this case if they have at least 1 edge)
    network.present <- network.present +
outer((rowSums(network.boot)>0),(rowSums(network.boot)>0),"*")
  }
  # End bootstrap

  # Calculate proportion of times observed in the same community
  P <- network.community/network.present
  P[!is.finite(P)] <- 0
  P

  # Calculate assortment from known community membership
  rc <- assortment.discrete(P,community.observed$membership)$r
  rc
  return(rc)
}
#end function

# run the function
calc_rc(giraffe_gbi, n.bootstraps=1000, plot.result=F)
rc

mean(network.boot)
mean(network)
modularity(community.boot)
modularity(community.observed)
```

```
##############################################################################################
### 5. Run SNA for each community
##############################################################################################

### Example with Community 1

COM1 <- giraffe[giraffe$Community=="1", ]
giraffe_gbi_comm1 <- get_group_by_individual(COM1, data_format = c("individuals"))
giraffe_network_comm1 <- get_network(giraffe_gbi_comm1, data_format = "GBI", association_index =
"SRI")
mean(giraffe_network_comm1) # tells us mean edge weights
sd(giraffe_network_comm1)
mean(giraffe_network_comm1>0) # mean non-zero edge weights
sd(giraffe_network_comm1>0)

# I calculated edge weight CVs from 1000 randomized networks
observed_cv_1 <- cv(giraffe_network_comm1)
networks.random <- network_permutation(association_data=giraffe_gbi_comm1,
                            data_format = "GBI",  permutations=permutations, returns=1, association_index
                            = "SRI",
                            association_matrix=giraffe_network_comm1, days=giraffe$Occasion,
within_day=TRUE)
random_cv_1 <- rep(NA, permutations)
for (i in 1:permutations) {
  random_cv_1[i] <- cv(networks.random[i,1:34,1:34])  ## 34 females in Community 1
}
observed_cv_1
mean(random_cv_1)
par(mfrow=c(1,2))
hist(random_cv_1, breaks=100, xlab="Random edge weight CV", main="Random Vs Observed
Community 1", xlim=c(1.35,1.8))
abline(v=observed_cv_1, col="red")
#the p-value is the number of times the CV value of the observed network is smaller than a
#randomized network, divided by the number of randomizations
sum(abs(observed_cv_1) < abs(random_cv_1))/10000
str(random_cv_1)

##############################################################################################
###### 6. Run General Linear Models for Social Differentiation (edge weight CV)
##############################################################################################

# import data; here I created a dataset with the observed edge weight CVs and edge weight CVs from
# the 1000 randomized networks, see above
giraffemodels.obs <- read.csv("edgeweightCVs_observed.csv)
giraffemodels.obs$Community <- as.factor(giraffemodels.obs$Community)
giraffemodels.rand <- read.csv("edgeweightCVs_random.csv")
giraffemodels.rand$Community <- as.factor(giraffemodels.rand$Community)

# run the model
ew.cv.obs <- glm(EW.CV ~ PopDen + Dist_boma + Dist_town + Prop_gv, family=gaussian,
data=giraffemodels.obs)
```

```
summary(ew.cv.obs)
# extract the coefficients for the effect of observed data
ew.cv.obs.coef <- coefficients(glm(EW.CV ~ PopDen + Dist_boma + Dist_town + Prop_gv,
                        family=gaussian, data=giraffemodels.obs))
ew.cv.obs.coef

# create storage space for 10000 random values of each coefficient:
ew.cv.rand.coef <- matrix(NA, nrow=10000, ncol=length(ew.cv.obs.coef))
ew.cv.rand.coef

# extract each random dataset and run the model
for (i in 1:10000) {
  # subset the dataset for the current randomization
  gm.rand <- giraffemodels.rand[which(giraffemodels.rand$Randomization==i),]

  # run the model and extract coefs and store as the current row of the results table
  ew.cv.rand.coef[i,] <- coefficients(glm(EW.CV ~ PopDen + Dist_boma + Dist_town + Prop_gv,
                                family=gaussian, data=gm.rand))
}

# obtain p-value for each coef and plot these – the number of times EWCV was less than random
par(mfrow=c(2,2))
Ps <- rep(NA, length(ew.cv.obs.coef))
for (i in 1:length(ew.cv.obs.coef)) {
  Ps[i] <- sum(ew.cv.obs.coef[i]<ew.cv.rand.coef[,i])/nrow(ew.cv.rand.coef)
  if (i > 1) { # avoid plotting intercept so that it fits neatly on 2 x 5 panels
    plot(ew.cv.rand.coef[,i], type='l', main=names(ew.cv.obs.coef)[i], xlab="Frequency",
ylab="Coefficients of randomized edge weight CV")
    abline(h=ew.cv.obs.coef[i], col="red")
  }
}
Ps
```

```
##############################################################################################
### R code for Chapter 5: “Leaving Without Going Anywhere?”
### MONICA L. BOND ET AL. UNIVERSITY OF ZURICH
##############################################################################################

# Load libraries
library(sp)
library(adehabitatLT)
library(lattice)
library(nlme)
library(rgdal)

nd1 <- read.csv("C:/YOURDATA.csv")
nd1$id <- factor(nd1$id)

#' Create a date-time object-> see '?strptime' for format options
nd1$datetime <- as.POSIXct(strptime(as.character(nd1$datetime),"%Y:%m:%d %H:%M:%S",
tz="Africa/Nairobi"))

#' Order chronologically by individual and datetime
nd1 <- nd1[order(nd1$id, nd1$datetime), ]
table(nd1$id)

#' ### Create a Spatial Object
#' Specify which columns have to be taken as coordinates
coordinates(nd1) <- ~Easting+Northing
head(nd1@data)
head(nd1@coords)

#' Define the coordinate system
proj4string(nd1) <- CRS("+proj=longlat +datum=WGS84")

#' Transform the coordinates system
#' -> first define it with proj4string, then transform it
nd1 <- spTransform(nd1, CRS("+proj=utm +zone=37 +south +ellps=WGS84"))
head(nd1)
plot(nd1)

# Transform the nd1 dataset back from a SpatialPointsDataFrame to a data frame, then order it
summary(nd1)
nd2 <- as.data.frame(nd1)
nd3 <- nd2[order(nd2$id,nd2$datetime),]
summary(nd3)

# Transform dataframe to a list, then use sapply(), to speed up the calculations of NSD
# so, here the NSD applied to the giraffe data is (x-x[1])^2 + (y-y[1])^2

nd3LS <- split(nd3, list(nd3$id))  #dataframe for each individual, then make as a list; then apply sapply

#calculate net squared displacement
NSD <- sapply(nd3LS, function(x) {
```

```
  nsd <- (x$Easting - x$Easting[1])^2 + (x$Northing - x$Northing[1])^2
})

# check the values obtained, make sure there are no mistakes
sapply(NSD,summary)
apply(sapply(NSD,summary),2,sqrt)

## now add back NSD values to the dataframe
# transform back into a dataframe

NSDdf <- data.frame(  id = as.factor(rep(names(sapply(NSD,function(x) length(x))),
as.numeric(sapply(NSD,function(x) length(x))))),
                    NSD = as.numeric(unlist(NSD))
)

all.equal(nd3$id, nd3$id)
# --> TRUE

## Unlist() the NSD values and add them to the existing nd3 dataframe;
# transforms things in a long list into a vector but things must be ordered in the correct way

nd3$NSD = as.numeric(unlist(NSD))

## NSDdf is not needed, hence we can delete it
rm(NSDdf)

# calculate days from first location for each individual, then add to the DF
nDays <- sapply(nd3LS, function(x) {
    nday <- (x$datetime - min(x$datetime))
})

nd3$nDays = as.numeric(unlist(nDays))

rm(nDays)

# plot the NSD patterns

xyplot(NSD~nDays, groups = id, data=nd3, type=c("l"), xlab="Number of days", ylab="Distance from
first detection")
```

Bibliography

Alberts, S.C. (2019). Social influences on survival and reproduction: Insights from a long-term study of wild baboons. *Journal of Animal Ecology*, 88, 47–66.

Alexander, R.D. (1974). The evolution of social behavior. *Annual Review of Ecological Systems*, 5, 325–383.

Anderson, B.S., Butts, C., & Carley, K. (1999). The interaction of size and density with graph-level indices. *Social Networks*, 21, 239–267.

Armitage, K.B., Van Vuren, D.H., Ozgul, A., & Oli, M.K. (2011). Proximate causes of natal dispersal in female yellow-bellied marmots, *Marmota flaviventris*. *Ecology*, 92, 218–227.

Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Connor, R., Di Fiore, A., Dunbar, R.I.M., Henzi, S.P., Holekamp, K., Korstjens, A.H., Layton, R., Lee, P., Lehmann, J., Manson, J.H., Ramos-Fernandez, G., Strier, K.B., & van Schaik, C.P. (2008). Fission-fusion dynamics: New research frameworks. *Current Anthropology* 49, 627–654. doi:10.1086/586708

Ball, M.C., Finnegan, L., Manseau, M., & Wilson, P. (2010). Integrating multiple analytical approaches to spatially delineate and characterize genetic population structure: an application to boreal caribou (*Rangifer tarandus caribou*) in central Canada. *Conservation Genetics*, 11, 2131–2143. doi:10.1007/s10592-010-0099-3

Barocas, A., Illany, A., Koren, L., Kam, M., & Geffen, E. (2011). Variance in centrality within rock hyrax social networks predicts adult longevity. *PLoS ONE*, 6:e22375. doi: 10.1371/journal.pone.0022375.

Bartoń, K. (2019). MuMIn: Multi-Model Inference. R package version 1.43.6. https://CRAN.R-project.org/package=MuMIn.

Bejder, L., Fletcher, D., & Bräger, S. (1998). A method for testing association patterns of social animals. *Animal Behaviour*, 56, 719–725.

Belton, L.E., Cameron, E.Z., & Dalerum, F. (2018). Social networks of spotted hyaenas in areas of contrasting human activity and infrastructure. *Animal Behaviour*, 135, 13–23.

Bercovitch F.B., & Berry P.S.M. (2009). Ecological determinants of herd size in the Thornicroft's giraffe of Zambia. *African Journal of Ecology*, 48, 962–971.

Bercovitch, F.B., & Berry, P.S.M. (2012). Herd composition, kinship, and fission-fusion social dynamics among wild giraffe. *African Journal of Ecology*, 51, 206–216. doi.org/10.1111/aje.12024

Bercovitch, F.B., & Berry, P.S.M. (2016). Life expectancy, maximum longevity, and lifetime reproductive success in female Thornicroft's giraffe in Zambia. *African Journal of Ecology*, 55, 443–450.

Berry, P.S.M. (1978). Range movements of giraffe in the Luangwa Valley, Zambia. *East African Wildlife Journal*, 16, 77–83.

Berry, P.S.M., & Bercovitch, F.B. (2015). Leadership of herd progressions in the Thornicroft's giraffe of Zambia. *African Journal of Ecology*, 53, 175–182.

Binagman Lackey, L.B. (2009). Giraffe studbook *Giraffa camelopardalis* North American Regional/Global. Association of Zoos and Aquariums and Disney's Animal Kingdom, Orlando, FL.

Bishop, L.C., Barham, L., Ditchfield, P.W., Elton, S., Harcourt-Smith, W.E.H., & Dawkins, P. (2016). Quaternary fossil fauna from the Luangwa Valley, Zambia. *Journal of Quaternary Science*, 31, 178–190.

Bivand, R. (2018). rgeos. Interface to geometry engine: Open source ('GEOS'). (R package version 0.3-28). http://CRAN.R-project.org/package=rgeos.

Blumstein, D.T. (2013). Yellow-bellied marmots: insights from an emergent view of sociality. *Philosophical Transactions of the Royal Society B*, 368, 20120349. doi.org/10.1098/rstb.2012.0349

Blumstein, D.T., Wey T.W., & Tang, K. (2009). A test of the social cohesion hypothesis: Interactive female marmots remain at home. *Proceedings: Biological Sciences*, 276, 3007–3012.

Bolger, D.T., Morrison, T.A., Vance, B., Lee, D.E., & Farid, H. (2012). A computer-assisted system for photographic mark-recapture analysis. *Methods in Ecology and Evolution*, 3, 812–822. doi.org/10.1111/j.2041-210X.2012.00212.x

Bolger, D., Ogutu, J., Strauss, M., Lee, D.E., Muneza, A., Fennessy, J., & Brown, D. (2019). *Giraffa camelopardalis* ssp. *tippelskirchi*. The IUCN Red List of Threatened Species 2019: e.T88421036A88421121.

Bond, M.L., König, B., Lee, D.E., Ozgul, A., & Farine, D.R. (in revision). Proximity to humans affects local social structure in a giraffe metapopulation. *Journal of Animal Ecology*.

Bond, M.L., Lee, D.E., Ozgul, A., & König, B. (2019). Fission-fusion dynamics of a megaherbivore are driven by ecological, anthropogenic, temporal, and social factors. *Oecologia*, 191, 335–347. doi:10.1007/s00442-019-04485-y

Bond, M.L., König, B., Ozgul, A., Farine, D.R., & Lee, D.E. (in review). Drivers of life-history variation in a giraffe metapopulation: the role of environmental versus social factors. *Journal of Animal Ecology*.

Bonenfant, C., Gaillard, J.-M., Coulson, T., Festa-Bianchet, M., Loison, A., Garel, M., Egil Loe, L., Blanchard, P., Pettorelli, N., Owen-Smith, N., du Toit, J., & Duncan, P. (2009). Empirical evidence of density-dependence in populations of large herbivores. *Advances in Ecological Research*, 41, 313–357.

Börger, L., & Fryxell. J.M. (2012). Quantifying individual differences in dispersal using net squared displacement. In Dispersal ecology and evolution (eds J. Clobert, M. Baguette, T.G. Benton, and J. M. Bullock). Pages 222–228. Oxford University Press.

Börger, L., Dalziel, B.D., & Fryxell, J.M. (2008). Are there general mechanisms of animal home range behavior? A review and prospects for future research. *Ecology Letters*, 11, 637–650.

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S., & Coulson, T. (2006). Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*, 75, 1393–1405.

Borner, M. (1985). The increasing isolation of Tarangire National Park. *Oryx*, 19, 91–96.

Bremner-Harrison, S., Prodohl, P.A., & Elwood, R.W. (2004). Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*). *Animal Conservation*, 7, 313–320.

Bretz, F., Hothorn T., & Westfall, P. (2010). Multiple Comparisons Using R, CRC Press, Boca Raton, Florida, USA.

Burnham, K.P., & Anderson, D.R. (2002). Model selection and multimodel inference: a practical information-theoretical approach. Springer-Verlag, New York, New York, USA.

Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C., & Pollock, K.H. (1987). Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph No. 5. Bethesda, Maryland, USA. 437 pp. doi.org/10.1002/rrr.3450040111

Burt, W.H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, 24, 346–352.

Butts, C.T. (2016). sna: Tools for Social Network Analysis. R package version 2.4. https://CRAN.R-project.org/package=sna

Cairns, J.S., & Schwager, S.J. (1987). A comparison of association indices. *Animal Behaviour*, 35, 1454–1469. doi.org/10.1016/S0003-3472(87)80018-0

Caister, L.E., Shields, W.M., & Gosser, A. (2003). Female tannin avoidance: A possible explanation for habitat and dietary segregation of giraffes (*Giraffa camelopardalis peralta*) in Niger. *African Journal of Ecology*, 41, 201–210.

Calenge, C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 516–519. doi.org/10.1016/j.ecolmodel.2006.03.017

Cameron, E.Z., Setsaas, T.H., & Linklater, W.L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences* 106, 13850–13853.

Cantor, M., Wedekin, L.L., Guimarães, P.R., Daura-Jorge, F.G., Rossi-Santos, M.R., & Simões-Lopes, P.C. (2012). Disentangling social networks from spatiotemporal dynamics: the temporal

structure of a dolphin society. *Animal Behaviour*, 84, 641–651. doi.org/10.1016/j.anbehav.2012.06.019

Carey, A.B., Reid, J.A., & Horton, S.P. (1990). Spotted owl home range and habitat use in southern Oregon Coast Ranges. *Journal of Wildlife Management*, 54, 11–17.

Carter, K.D., Seddon, J.M., Frère, C.H., Carter, J.K., & Goldizen, A.W. (2013a). Fission-fusion dynamics in wild giraffes may be driven by kinship, spatial overlap and individual social preferences. *Animal Behaviour*, 85, 385–394. doi.org/10.1016/j.anbehav.2012.11.011

Carter, K.D., Brand, R., Carter, J.K., Shorrocks, B., & Goldizen, A.W. (2013b). Social networks, long-term associations and age-related sociability of wild giraffes. *Animal Behaviour*, 86, 901–910. doi.org/10.1016/j.anbehav.2013.08.002

Caswell, H. (2002). Matrix population models. Sinauer and Associates, Inc., Sunderland Massachusetts, USA.

Cederlund, G., & Sand, H. (1994). Home range size in relation to age and sex in moose. *Journal of Mammalogy*, 75, 1005–1012.

Ceballos, G., Ehrlich, P.R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, E6089–E6096.

Chapman, C.A., & Chapman, L J. (2000). Determinants of Group Size in Primates: The Importance of Travel Costs. In: On the Move: How and Why Animals Travel in Groups. Boinski S, Garber PA (eds) University of Chicago Press, Chicago), pp 24–42.

Cibien, C., & Sempere, A. (1989). Food availability as a factor in habitat use by roe deer. *Acta Theriologica*, 34, 111–123.

Clobert, J., Danchin, E., Dhondt, A.A., & Nichols, J.D. (2001). Dispersal. Oxford University Press, Oxford.

Clutton-Brock, T.H. (2016). Mammal Societies. Wiley-Blackwell, Sussex, UK.

Clutton-Brock, T.H., & Isvaran, K. (2007). Sex differences in ageing in natural populations of vertebrates. *Proceedings of the National Academy of Sciences Biological Sciences*, 274, 3097–3104. doi:10.1098/rspb.2007.1138

Clutton-Brock, T., & Sheldon, B.C. (2010). Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology and Evolution*, 25, 562–573. doi.org/10.1016/j.tree.2010.08.002

Clutton-Brock, T., Iason, G.R., & Guinness, F.E. (1987). Sexual segregation and density-related changes in habitat use in male and female red deer (*Cervus elaphus*). *Journal of Zoology*, 211, 275–289.

Coe, M.J., Cumming, D.H., & Phillipson, J. (1976). Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia*, 22, 341–354.

Conradt, L., Clutton-Brock, T.H., & Guinness, F.E. (1999). The relationship between habitat choice and lifetime reproductive success in female red deer. *Oecologia*, 120, 218–224. doi.org/10.1007/s004420050851

Contasti, A.L., Tissier, E.J., Johnstone, J.F., & McLoughlin, P.D. (2012). Explaining spatial heterogeneity in population dynamics and genetics from spatial variation in resources for a large herbivore. *PLoS One*, doi.org/10.1371/journal.pone.0047858

Cooch, E.G., & White, G.C. (2019). Program MARK: A gentle introduction. 19th edition.

Coulson, T., Albon, S., Pilkington, J. & Clutton-Brock, T. (1999). Small-scale spatial dynamics in a fluctuating ungulate population. *Journal of Animal Ecology*, 69, 658–671. doi.org/10.1046/j.1365-2656.1999.00298.x

Croft, D.P., James, R., & Krause, J. (2008). Exploring animal social networks. Princeton University Press, Princeton, New Jersey, USA.

Croft, D.P., Madden, J.R., Franks, D.W., & James, R. (2011). Hypothesis testing in animal social networks. *Trends in Ecology and Evolution*, 26, 502–507.

Csárdi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal for Complex Systems* 1695.

Dagg, A.I. (1971). *Giraffa camelopardalis*. Mammalian Species 5, 1–8.

Dagg, A.I. (2014) Giraffe biology, behavior and conservation. Cambridge University Press, New York, New York, USA.

Dagg A.I., & Foster, J.B. (1976). The Giraffe: Its Biology, Behavior, and Ecology. Van Nostrand Reinhold, New York.

Davis, G.H., Crofoot, M.C., & Farine, D.R. (2018). Estimating the robustness and uncertainty of animal social networks using different observational methods. *Animal Behaviour*, 141, 29–44. doi.org/10.1016/j.anbehav.2018.04.012

Deacon, F., & Smit, N. (2017). Spatial ecology and habitat use of giraffe (*Giraffa camelopardalis*) in South Africa. *Basic and Applied Ecology*, 21, 55–65.

Dechen Quinn, A.C., Williams, D.M., & Porter, W.F. (2013). Landscape structure influences space use by white-tailed deer. *Journal of Mammalogy*, 94, 398–407.

del Castillo, S.M., Bashaw, M.J., Patton, M.L., Rieches, R.R., & Bercovitch, F.B. (2005). Fecal steroid analysis of female giraffe (*Giraffa camelopardalis*) reproductive condition and the impact of endocrine status on daily time budgets. *General and Comparative Endocrinology*, 141, 271–281

Devillard, S., & Bray, Y. (2009). Assessing the effect on survival of natal dispersal using multistate capture-recapture models. *Ecology* 90, 2902–2912

Dhondt, A.A. (2001). Tradeoffs between reproduction and survival in tits. *Ardea*, 89, 155–166. doi:10.2307/4837

Dillon, A., & Kelly, M.J. (2008). Ocelot home range, overlap and density: Comparing radio telemetry with camera trapping. *Journal of Zoology*, 275, 391–398.

Dobson, F.S. (1982). Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour*, 30, 1185–1192.

du Toit, J.T. (1990). Home range-body mass relations: A field study on African browsing ruminants. *Oecologia*, 85, 301–303.

du Toit, J.T., & Cumming, D.H.M. (1999). Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation*, 8, 1643–1661.

Dublin, H.T., Sinclair, A.R.E., & McGalde, J. (1990). Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology* 59, 1147–1164.

Dunbar, R.I.M., & Shultz, S. (2010). Bondedness and sociality. *Behaviour* 147, 775–803.

Ebensperger, L.A., Aracena, S., Avendaño, N., Toro, A., León, C., Ramírez-Estrada, J., & Abades, S. (2017). Social instability decreases alloparental care and quality of weaned offspring in a communally rearing rodent. *Animal Behaviour*, 113, 195–205.

Edenbrow, M., Darden, S.K., Ramnarine, I.W., Evans, J.P., James, R., & Croft, D.P. (2011). Environmental effects on social interaction networks and male reproductive behaviour in guppies, *Poecilia reticulata*. *Animal Behaviour*, 81, 551–558.

Ekernas, L.S., & Cords, M. (2007). Social and environmental factors influencing natal dispersal in blue monkeys, *Cercopithecus mitis stuhlmanni*. Anim. Behav. 73, 1009–1020.

Ellis, S., Snyder-Mackler, N., Ruiz-Lambides, A., Platt, M.L., and Brent, L.J.N. (2019). Deconstructing sociality: the types of social connections that predict longevity in a group-living primate. *Proceedings of the Royal Society B*, 286, 20191991. doi:10.1098/rspb.2019.1991.

Ellison, A.M. (1996). An introduction to Bayesian inference for ecological research and environmental decision making. *Ecological Applications* 6, 1036–1046.

Estes, R.D. (1991). The Behavior Guide to African Mammals. University of California Press, Berkeley, CA.

Farine, D.R. (2013). Animal social network inference and permutations for ecologists in R using asnipe. *Methods in Ecology and Evolution*, 4, 1187–1194. doi.org/10.1111/2041-210X.12121

Farine, D.R. (2016). assortnet: Calculate the Assortativity Coefficient of Weighted and Binary Networks. R package version 0.12. https://CRAN.R-project.org/package=assortnet

Farine, D.R. (2017). A guide to null models for animal social network analysis. *Methods in Ecology and Evolution*, 8, 1309–1320.

Farine, D.R., & Aplin, L.M. (2019). Spurious inference when comparing networks. bioRxiv doi: doi.org/10.1101/619957.

Farine, D.R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology*, 84, 1144–1163. doi.org/10.1111/1365-2656.12418

Farine, D.R., Montiglio, P.-O., & Spiegel, O. (2015). From individuals to groups and back: The evolutionary implications of group phenotypic composition. *Trends in Ecology and Evolution*, 30, 609–621. doi.org/10.1016/j.tree.2015.07.005

Fennessy, J. (2009). Home range and seasonal movements of *Giraffa camelopardalis angolensis* in the northern Namib Desert. *African Journal of Ecology*, 47, 318–327.

Fieberg, J. (2007). Kernel density estimators of home range: Smoothing and the autocorrelation red herring. *Ecology*, 88, 1059–1066.

Fieberg, J., & Börger, L. (2012). Could you please phrase "home range" as a question? *Journal of Mammalogy*, 93, 890–902.

Foley, C.A.H., & Faust, L.J. (2010). Rapid population growth in an elephant *Loxodonta africana* population recovering from poaching in Tarangire National Park, Tanzania. *Oryx*, 44, 205–212. doi.org/10.1017/S0030605309990706

Fortin D., Fortin, M.-E., Beyer, H.L., Duchesne, T., Courant, S., & Dancose, K. (2009). Group-size-mediated habitat selection and group fusion-fission dynamics of bison under predation risk. *Ecology*, 90, 2480–2490.

Fortunato, S. (2010). Community detection in graphs. *Physics Reports*, 486, 75–174. doi.org/10.1016/j.physrep.2009.11.002

Foster, J.B. (1966). The giraffe of Nairobi National Park: home range, sex ratios, the herd, and food. *East African Wildlife Journal*, 4, 139–148. doi.org/10.1111/j.1365-2028.1966.tb00889.x

Foster, J.B., & Dagg, A.I. (1972). Notes on the biology of the giraffe. *African Journal of Ecology*, 10, 1–16.

Frank, D.A., & McNaughton, S.J. (1992). The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. *Ecology*, 76, 2043–2058.

Franks, D.W., Ruxton, G.D., & James, R. (2010). Sampling animal association networks with the gambit of the group. *Behavioral Ecology and Sociobiology*, 64, 493–503.

Frederiksen, M., Harris, M.P., & Wanless, S. (2005). Inter-population variation in demographic parameters: a neglected subject? *Oikos*, 111, 209–214. doi.org/10.1111/j.0030-1299.2005.13746.x

Frère, C.H., Krützen, M., Mann, J., Connor, R.C., Bejder, L., & Sherwin, W.B. (2010). Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proceedings of the National Academy of Sciences* 107, 19949–19954.

Fretwell, S.D., & Lucas, H.L.J. (1970). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, 19, 16–36.

Furstenburg, D., & van Hoven, W. (1994) Condensed tannin as anti-defoliate agent against browing by giraffe (*Giraffa camelopardalis*) in the Kruger National Park. *Comparative Biochemical Physiology*, 107A, 425–431.

Gaillard, J.M., Festa-Bianchet, M., & Yoccoz, N.G. (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, 13, 58–63. doi.org/10.1016/S0169-5347(97)01237-8

Gaillard, J.M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., & Toïgo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, 31, 357–93. doi.org/10.1146/annurev.ecolsys.31.1.367

Gaillard, J.M., Hewison, A.J.M., Kjellander, P., Pettorelli, N., Bonenfant, C., Van Moorter, B., Liberg, O., Andren, H., Van Laere, G., Klein, F., Angibault, J.-M., Coulon, A., & Vanpé, C. (2008). Population density and sex do not influence fine-scale natal dispersal in roe deer. *Proceedings of the Royal Society B*, 275, 2025–2030.

Ginnett, T.F., & Demmett, M.W. (1999). Sexual segregation by Masai giraffes at two spatial scales. *African Journal of Ecology*, 37, 93–106.

Girvan, M., & Newman, M.E.J. (2002). Community structure in social and biological networks. *Proceedings of the National Academy of Sciences USA*, 99, 7821. doi.org/10.1073/pnas.122653799

Glenn, E.M., Hansen, M.C., & Anthony, R.G. (2004). Spotted owl home-range and habitat use in young forests of western Oregon. *Journal of Wildlife Management*, 68, 33–50.

Gobush, K.S., & Wasser, S.K. (2009). Behavioural correlates of low relatedness in African elephant core groups of a poached population. *Animal Behaviour*, 78, 1079–1086.

Greenwood, P.J. (1980). Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour, 28, 1140–1162.

Grosbois, V., Harris, M.P., Anker-Nilssen, T., McCleery, R.H., Shaw, D.N., Morgan, B.J.T., & Gimenez, O. (2009). Modeling survival at multi-population scales using mark–recapture data. *Ecology*, 90, 2922–2932. doi.org/10.1890/08-1657.1

Hamilton, W.D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, 31, 295–311.

Hansen, R.M., Mugambi, M.M., & Bauni, S.M. (1985). Diets and trophic ranking of ungulates of the northern Serengeti. *Journal of Wildlife Management*, 49, 823–829. doi:10.2307/3801717

Hanski, I. (1999). Metapopulation Ecology. Oxford University Press, New York, New York, USA.

Hadfield, J.D. (2010). MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. *Journal of Statistical Software*, 33, 1–22

Harestad, A.S., & Bunnell, F.L. (1979). Home range and body weight: A reevaluation. *Ecology*, 60, 389–402.

Harwood, T.D. (2009). The circular definition of populations and its implications for biological sampling. *Molecular Ecology*, 18, 765–768. doi.org/10.1111/j.1365-294X.2008.04066.x

He, P., Maldonado-Chaparro, A.A., & Farine, D.R. (2019). The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. *Behavioral Ecology and Sociobiology*, 73, 9–23.

Hijmans, R.J., & van Etten, J. (2012). raster: Geographic analysis and modeling with raster data. R package version 2.0-12. http://CRAN.R-project.org/package=raster.

Holekamp, K.E., Smith, J.E., Strelioff, C.C., Van Horn, R.C., & Watts, H.E. (2012). Society, demography and genetic structure in the spotted hyena. *Molecular Ecology*, 21, 613–632.

Hopcraft, J.G., Sinclair, A.R.E., & Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, 74, 559–566. doi.org/10.1111/j.1365-2656.2005.00955.x

Hoppitt, W.J.E., & Farine, D.R. (2018). Association indices for quantifying social relationships: how to deal with missing observations of individuals or groups. *Animal Behaviour* 136, 227–238.

House, J.S., Landis, K.R., & Umberson, D. (1988). Social relationships and health. *Science*, 241, 540–545.

Jarman, P.J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour*, 58, 215–267.

Jennrich, R.I., & Turner, F.B. (1969). Measurement of non-circular home range. *Journal of Theoretical Biology*, 22, 227–237.

Jorgenson, J.T., Festa-Bianchet, M., Gaillard, J.M., & Wishart, W.D. (1997). Effects of age, sex, disease, and density on survival of bighorn sheep. *Ecology*, 78, 1019–1032. doi.org/10.1890/0012-9658(1997)078[1019:EOASDA]2.0.CO;2

Kahurananga, J., & Silkiluwasha, F. (1997). The migration of zebra and wildebeest between Tarangire National Park and Simanjiro Plains, northern Tanzania, in 1972 and recent trends. *African Journal of Ecology*, 35, 179–185.

Kavwele, C.M., Kimanzi, J.K., & Kinyanjui, M.J. (2017). Impacts of bush encroachment on wildlife species diversity, composition, and habitat preference in Ol Pejeta Conservancy, Kaikipia, Kenya. *International Journal of Ecology*, 2017, 5620125. https://doi.org/10.1155/2017/5620125.

Kie, J.G., Bowyer, R.T., Nicholson, M.C., Boroski, B.B., & Loft, E.R. (2002). Landscape heterogeneity at differing scales: Effects on spatial distribution of mule deer. *Ecology*, 83, 530–554.

Kiffner, C., Peters, L., Stroming, A., & Kioko, J. (2015). Bushmeat consumption in the Tarangire-Manyara Ecosystem, Tanzania. *Tropical Conservation Science* 8, 318–332.

Kindt, R.J., Lillesø, P.B. van Breugel, P., Bingham, M., Sebsebe, D., Dudley, C., Friis, I., Gachathi, F., Kalema, J., Mbago, F., Minani, V., Moshi, H.N., Mulumba, J., Namaganda, M., Ndangalasi, H.J., Ruffo, C.K., Jamnadass, R., & Graudal, L. (2011). Potential natural vegetation of eastern Africa. Vol. 4 and 5. Description and tree species composition for potential natural vegetation types. Forest & Landscape Working Paper 65-2011. downloaded from http://vegetationmap4africa.org/2_Vegetation_map.html

Kissui, B.M. (2008). Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. *Animal Conservation* 11, 422–432.

Kjellander, P., Gaillard, J.M. Hewison, M., & Liberg, O. (2004). Predation risk and longevity influence variation in fitness of female roe deer (*Capreolus capreolus L.*) *Proceedings of Royal Society B*, 271, S338–S340.

Kjellander, P., Hewison, A.J.M., Liberg, O., Angibault, J.M., Bideau, E., & Cargnelutti, B. (2004). Experimental evidence for density-dependence of home-range size in roe deer (*Capreolus capreolus L.*): Comparison of two long-term studies. *Oecologia*, 139, 478–485.

Knüsel, M.A., Lee, D.E., König, B., & Bond, M.L. (2019). Correlates of home-range size of giraffes *Giraffa camelopardalis*. *Animal Behaviour* 149, 143–151. doi.org/10.1016/j.anbehav.2019.01.017

Krause, J., & Ruxton, G.D. (2002). Living in Groups. Oxford University Press, Oxford, UK.

Kummer, H. (1971). Primate societies: group techniques of ecological adaptation. Chicago: Aldine

Kurvers, R.H.J.M., Krause, J., Croft, D.P., Wilson, A.D.M., & Wolf, M. (2014). The evolutionary and ecological consequences of animal social networks: emerging issues. *Trends in Ecology and Evolution* 26, 326–335.

Lamprey, H.F. (1963). The Tarangire Game Reserve. *Tanganyika Notes and Records* 60, 10–22.

Lamprey, H.F. (1964). Estimation of the large mammal densities, biomass and energy exchange in the Tarangire game reserve and the Maasai steppe in Tanganyika. *East African Wildlife Journal*, 1, 3–92. doi.org/10.1111/j.1365-2028.1964.tb00194.x

Langman, V.A. (1977). Cow-calf relationships in giraffe (*Giraffa camelopardalis giraffa*). *Zeitschrift für Tierpsychologie* 43, 264–286.

Lattanzio, M.S., & Miles, D.B. (2014). Ecological divergence among colour morphs mediated by changes in spatial network structure associated with disturbance. *Journal of Animal Ecology*, 83, 1490–1500.

Le Pendu, Y., & Ciofolo, I. (1999). Seasonal movements of giraffes in Niger. *Journal of Tropical Ecology*, 15, 341–353.

Le Pendu, Y., Ciofolo, I., & Gosser, A. (2000). The social organization of giraffes in Niger. *African Journal of Ecology*, 38, 78–85.

Lebreton, J.-D., Burnham, K.P., Clobert, J., & Anderson, D.R. (1992). Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs*, 62, 67–118.

Lee, D.E. (2018). Evaluating conservation effectiveness in a Tanzanian community wildlife management area. *Journal of Wildlife Management* 82, 1767–1774. doi.org/10.1002/jwmg.21549

Lee, D.E., & Bolger, D.T. (2017). Movements and source-sink dynamics of a Masai giraffe metapopulation. *Population Ecology*, 59, 157–168. doi:10.1007/s10144-017-0580-7

Lee, D.E., & Bond, M.L. (2018). Quantifying the ecological success of a community-based wildlife conservation area in Tanzania. *Journal of Mammalogy*, 99, 459–464.

Lee, D.E., & Strauss, M.K.L. (2016) Giraffe Demography and Population Ecology. Reference Module in Earth Sciences and Environmental Studies. doi: 10.1016/B978-0-12-409548-9.09721-9.

Lee, D.E., Bond, M.L., Kissui, B.M., Kiwango, Y.A., & Bolger, D.T. (2016a). Spatial variation in giraffe demography: a test of 2 paradigms. *Journal of Mammalogy*, 97, 1015–1025. doi.org/10.1093/jmammal/gyw086

Lee, D.E., Bond, M.L., & Bolger, D.T. (2017). Season of birth affects juvenile survival of giraffe. *Population Ecology*, 59, 45–54. doi 10.1007/s10144-017-0571-8

Lee, D.E., Fienieg, E., Van Oosterhout C., Muller, Z., Strauss, M., Carter, K.D., Scheijen, C.P.J., & Deacon, F. (2020). Giraffe translocation population viability analysis. *Endangered Species Research*, 41, 245-252.

Lee D.E., Kissui B.M., Kiwango Y.A., & Bond M.L. (2016b). Migratory herds of wildebeests and zebras indirectly affect calf survival of giraffes. *Ecology and Evolution*, 6, 8402–8411.

Leu, S.T., Farine, D.R., Wey, T.W., Sih, A., & Bull, C.M. (2016). Environment modulates population social structure: experimental evidence from replicated social networks of wild lizards. *Animal Behaviour*, 111, 23–31.

Leuthold, B.M. (1979). Social organization and behaviour of giraffe in Tsavo East National Park. *African Journal of Ecology* 17, 19–34.

Leuthold, W. (1976) Group size in elephants of Tsavo National Park and possible factors influencing it. *Journal of Animal Ecology*, 45, 425–439.

Leuthold, B., & Leuthold, W. (1978). Ecology of the giraffe in Tsavo East National Park, Kenya. *East African Wildlife Journal*, 16, 1–20.

Lichtenfeld, L.L. (2005). Our shared kingdom at risk: Human-lion relationships in the 21st century. PhD dissertation, Yale University.

Lindenmayer, D.B., & Fischer, J. (2013). Habitat fragmentation and landscape change: An ecological and conservation synthesis. Washington, D.C.: Island Press.

Linklater, W.L., & Cameron, E.Z. (2009). Social dispersal but with philopatry reveals incest avoidance in a polygynous ungulate. *Animal Behaviour* 77, 1085–1093.

Loe, L.E., Mysterud, A., Veiberg, V., & Langvatn, R. (2009). Negative density-dependent emigration of males in an increasing red deer population. *Proceedings of the Royal Society B*, 276, 251–2587.

Loison, A., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J. T., & Jullien, J.-M. (1999). Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology*, 80, 2539–2554. doi.org/10.1890/0012-9658(1999)080[2539:ASSIFP]2.0.CO;2

Lusseau, D., & Newman, M.E.J. (2004). Identifying the role that animals play in their social networks. *Proceedings of the Royal Society of London Series B*, 271, S477–S481.

Lusseau, D., Wilson, B., Hammond, P.S., Grellier, K., Durban, J.W., Parsons, K.M., Barton, T.R., & Thompson, P. M. (2006) Quantifying the influence of sociality on population structure in bottlenose dolphins. *Journal of Animal Ecology*, 75, 14–24. doi.org/10.1111/j.1365-2656.2005.01013.x

Majolo, B., De Bortoli Vizioli, A., & Schino, G. (2008). Costs and benefits of group living in primates: group size effects on behaviour and demography. *Animal Behaviour*, 76, 1235–1247.

Maldonado-Chaparro, A.A., Alarcon-Nieto, G., Klarevas-Irby, J.A., & Farine, D.R. (2018). Experimental disturbances reveal group-level costs of social instability. *Proceedings of the Royal Society B* 285, 20181577. doi.org/10.1098/rspb.2018.1577

Marjamäki, P.H., Contasti, A.L., Coulson, T.N., & McLoughlin, P. D. (2013). Local density and group size interacts with age and sex to determine direction and rate of social dispersal in a polygynous mammal. *Ecology and Evolution*, 3, 3073–3082.

Markham, A.C., Gesquiere, L.R., Alberts, S.C., & Altmann, J. (2015). Optimal group size in a highly social mammal. *Proceedings of the National Academy of Sciences*, 112, 14882–14887.

Maryanski, A.R. (1987). African ape social structure: is there strength in weak ties? *Social Networks*, 9, 191–215.

Mazerolle, M.J. (2019) AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.2-2. https://cran.r-project.org/package=AICcmodavg.

McFarland, R., Murphy, D., Lusseau, D., Henzi, S.P., Parker, J.L., Pollet, T.V., & Barrett, L. (2017). The 'strength of weak ties' among female baboons: fitness-related benefits of social bonds. *Animal Behaviour*, 126, 101–106.

McKnight, B.L. (2015). Relationship between group dynamics and spatial distribution of African elephants in a semi-arid environment. *African Journal of Ecology*, 53, 439–446.

McLoughlin, P.D., Gaillard, J.-M., Boyce, M.S., Bonenfant, C., Messier, F., Duncan, P., Delorme, D., Van Moorter, B., Saïd, S., & Klein, F. (2007). Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology*, 88, 3192–3201.

McNaughton, S.J. (1985). Ecology of a grazing ecosystem: The Serengeti. *Ecological Monographs*, 55, 259–294.

McNaughton, S.J., Ruess, R.W., & Seagle, S.W. (1988). Dynamics in African ecosystems: Herbivorous mammals affect primary productivity and regulate recycling balances. *BioScience*, 38, 794–800.

Mitchell, M.S., & Powell, R.A. (2012). Foraging optimally for home ranges. *Journal of Mammalogy*, 93, 917–928.

Mogensen, N.L., Ogutu, J.O., & Dabelsteen, T. (2011). The effects of pastoralism and protection on lion behaviour, demography, and space use in the Mara Region of Kenya. *African Ecology*, 46, 78–87.

Morellet, N., Bonenfant, C., Börger, L., Ossie, F., Cagnacci, F., Heurich, M., Kjellander, P., Linnell, J.D.C., Nicoloso, S., Sustr, P., Urbani, F., & Mysterud, A. (2013). Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. *Journal of Animal Ecology*, 82, 1326–39.

Moritz, C. (1994). Defining 'evolutionarily significant units' for conservation. *Trends in Evolution and Ecology*, 9, 373–375. doi:10.1016/0169-5347(94)90057-4.

Morris, W.F., & Doak, D.F. (2002). Quantitative conservation biology theory and practice of population viability analysis. Sinauer and Associates, Inc., Sunderland, Massachusetts, USA.

Morrison T.A., & Bolger D.T. (2014) Connectivity and bottlenecks in a migratory wildebeest *Connochaetes taurinus* population. *Oryx*, 48, 613–621.

Mramba R.P., Mahenya O., Siyaya A., Mathisen K.M., Andreassen H.P., & Skarpe C. (2017) Sexual segregation in foraging giraffe. *Acta Oecologica*, 79, 26–35.

Msoffe F.U., Said M.Y., Ogutu J.O., Kifugo S.C., de Leeuw J., van Gardingen P., Reid R.S. (2011). Spatial correlates of land-use changes in the Maasai-Steppe of Tanzania: Implications for conservation and environmental planning. *International Journal of Biodiversity Conservation*, 3, 280–290.

Msoffe, F.U., Kifugo, S.C., Said, M.Y., Ole Neselle, M., Van Gardingen, P., Reid, R.S., Ogutu, J.O., Herero, M., & de Leeuw, J. (2011). Drivers and impacts of land-use change in the Maasai

Steppe of northern Tanzania: an ecological, social and political analysis. *Journal of Land Use Science*, 6, 261–281. doi.org/10.1080/1747423X.2010.511682

Muller, Z. (2018). Population structure of giraffes is affected by management in the Great Rift Valley, Kenya. *PLoS One*, 13, c0189678.

Muller Z., Cuthill I.C., & Harris S. (2018). Group sizes of giraffes in Kenya: the influence of habitat, predation, and the age and sex of individuals. *Journal of Zoology*, 306, 77–87.

Muller, Z., Cantor, M., Cuthill, I.C., & Harris, S. (2018). Giraffe social preferences are context dependent. *Animal Behaviour* 146, 37–49.

Muller, Z., Bercovitch, F., Brand, R., Brown, D., Brown, M., Bolger, D., Carter, K., Deacon, F., Doherty, J.B., Fennessey, J., Fennessey, S., Hussein, A.A., Lee, D.E., Marais, A., Strauss, M., Tutchings, A., & Wube, T. (2018). *Giraffa camelopardalis* (amended version of 2016 assessment). IUCN Red List of Threatened Species, 2018, e.T9194A136266699. http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T9194A136266699.en.

Muller, Z., Cuthill, I.C., & Harris, S. (2019). Giraffe (*Giraffa camelopardalis*) social networks in areas of contrasting human activity and lion density. *Ethology*, 125,702–715. doi:10.1111/eth.12923

Nagy, J.A., Johnson, D.L., Larter, N.C., Campbell, M.W., Derocher, A.E., Kelly, A., Dumond, M., Allaire, D., & Croft, B. (2011). Subpopulation structure of caribou (*Rangifer tarandus L.*) in arctic and subarctic Canada. *Ecological Applications*, 21, 2334–2348. doi:10.1890/10-1410.1

Ndibalema, V.G. & Songorwa, A.N. (2007). Illegal meat hunting in Serengeti: dynamics in consumption and preferences. *African Journal of Ecology*, 46, 311–319.

Newman, M.E.J. (2003). Mixing patterns in networks. *Physical Review E*, 67, art, no. -026126. doi:10.1103/PhysRevE.67.026126

Newman, M.E.J. (2006). Modularity and community structure in networks. *Proceedings of the National Academy of Sciences*, 103, 8577–8582.

Newman, M.E.J., & Girvan, M. (2004). Finding and evaluating community structure in networks. *Physics Review E*, 69, 026113. doi.org/10.1103/PhysRevE.69.026113

Newmark, W.D. (2008). Isolation of African protected areas. *Frontiers in Ecology and the Environment*, 6, 321–328.

Nichols, J.D. (1992). Capture-recapture models using marked animals to study population dynamics. *BioScience*, 42, 94–102.

Nichols, J.D., Hines, J.E., Lebreton, J.-D., & Pradel, R. (2000). Estimation of contributions to population growth: a reverse-time capture-recapture approach. *Ecology*, 81, 3362–3376. oi.org/10.1890/0012-9658(2000)081[3362:EOCTPG]2.0.CO;2

Nilsen, E.B., Gaillard, J.-M., Andersen, R., Odden, J., Delorme, D., van Laere, G., & Linnell, J.D.C. (2009). A slow life in hell or a fast life in heaven: demographic analyses of contrasting

roe deer populations. *Journal of Animal Ecology*, 78, 585–594. doi:10.1111/j.1365-2656.2009.01523.x

Ofstad, E.G., Herfindal, I., Solberg, E.J., & Sæther, B.-E. (2016). Home ranges, habitat and body mass: Simple correlates of home range size in ungulates. *Proceedings of the Royal Society B*, 283, 20161234.

Ogutu, J.O., Piepho, H.P., Dublin, H.T., Bhola, N., & Reid, R.S. (2007). El Niño-Southern oscillation, rainfall, temperature, and normalized difference vegetation index fluctuations in the Mara-Serengeti ecosystem. *African Journal of Ecology*, 46, 132–143.

Owen-Smith, N. (1988). Megaherbivores: The Influence of Very Large Body Size on Ecology. Cambridge University Press, Cambridge, United Kingdom.

Owen-Smith, N. (2008). Changing vulnerability to predation related to season and sex in an African ungulate assemblage. *Oikos*, 117, 602–610.

Owen-Smith, N., & Marshall, J.P. (2010). Definitive case studies. In Dynamics of large herbivore populations in changing environments: towards appropriate models (ed. Owen-Smith, N.). Wiley-Blackwell, Oxford.

Ozgul, A., Armitage, K.A., Blumstein, D.T., & Oli, M.K. (2006). Spatiotemporal variation in survival rates: implications for population dynamics of yellow-bellied marmots. *Ecology*, 87, 1027–1037. doi:10.1890/0012-9658(2006)87[1027:svisri]2.0.co;2

Palmer, T.A., Stanton, M.L., Young, T.P., Goheen, J.R., Pringle, R.M., & Karban, R. (2008). Breakdown of an ant-plant mutualism follows the loss of large herbivores from an African savanna. *Science* 319, 192–195.

Papageorgiou, D., Christensen, C. Gall, G.E.C., Klarevas-Irby, J.A., Couzin, I.D., & Farine, D.R. (2019). The multilevel society of a small-brained bird. *Current Biology*, 29, R1105–R1121. doi.org/10.1016/j.cub.2019.09.072

Paradis, E., Baillie, S.R., Sutherland, W.J., Dudley, C., Crick, H.Q.P., & Gregory, R.D. (2000). Large-scale spatial variation in the breeding performance of song thrushes *Turdus philomelos* and blackbirds *T. merula* in Britain. *Journal of Applied Ecology*, 37, 73–87. doi.org/10.1046/j.1365-2664.2000.00547.x

Parmenter, R.R., Yates, T.L., Anderson, D.R., Burnham, K.P., Dunnum, J.L., Franklin, A.B., Friggens, M.T., Lubow, B.C., Miller, M., Olson, G.S., Parmenter, C.A., Pollard, J., Rexstad, E., Shenk, T.M., Stanley, T.R., & White, G.C. (2003). Small-mammal density estimation: a field comparison of grid-based vs. web-based density estimators. *Ecological Monographs*, 73, 1–26.

Parsons, K.M., Balcomb, K.C., Ford, J.K.B., & Durban, J.W. (2009). The social dynamics of southern resident killer whales and conservation implications for this endangered population. *Animal Behaviour*, 77, 963–971.

Pays, O., Benhamou, S., Helder, R., & Gerard, J.-F. (2007) The dynamics of group formation in large mammalian herbivores: an analysis in the European roe deer. *Animal Behaviour*, 74, 1429–1441.

Pépin, D., & Gerard, J.-F. (2008). Group dynamics and local population density dependence of group size in the Pyrenean chamois, *Rupicapra pyrenaica*. *Animal Behaviour*, 75, 361–369.

Pellew, R.A. (1984). Food consumption and energy budgets of the giraffe. *Journal of Applied Ecology*, 21, 141–159.

Pinter-Wollman, N., Isbell, L.A., & Hart, L.A. (2009). The relationship between social behaviour and habitat familiarity in African elephants (*Loxodonta africana*). *Proceedings of the Royal Society B*, 276, 1009–1014.

Pittet, F., Babb, J.A., Carini, L., & Nephew, B.C. (2017). Chronic social instability in adult female rats alters social behavior, maternal aggression and offspring development. *Developmental Psychobiology*, 59, 291–302.

Pollack, K.H. (1982). A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management*, 46, 752–757. doi:10.2307/3808568

Porter, M.A., Onnela, J., & Mucha, P.J. (2009). Communities in networks. *Notices of the American Mathematical Society*, 56, 1082–1166.

Powell, R.A. (2000). Animal home ranges and territories and home range estimators. In L. Boitani & T. K. Fuller (Eds.), Research techniques in animal ecology: Controversies and consequences (Chapter 3, pp. 65–103). New York, NY: Columbia University Press.

Powell, R.A., & Mitchell, M.S. (2012). What is a home range? *Journal of Mammalogy*, 93, 948–958.

Pradel, R. (1996). Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics*, 52, 703–709. doi:10.2307/2532908

Pratt, D.M., & Anderson, V.H. (1979). Giraffe cow-calf relationships and the social development of the calf in the Serengeti. *Zeitschrift fur Tierpsychologie*, 51, 233–251.

Pratt, D.M., & Anderson, V.H. (1985). Giraffe social behaviours. *Journal of Natural History*, 19, 771–781.

Prehn, S.G., Laesser, B.E., Calusen, C.G., Jonck, K., Dabelsteen, T. & Brask, J.B. (2019). Seasonal variation and stability across years in a social network of wild giraffe. *Animal Behaviour*, 157, 95–104.

Prins, H.H.T. (1987). Nature conservation as an integral part of optimal land use in East Africa: the case of the Masai Ecosystem of northern Tanzania. *Biological Conservation*, 40, 141–161. doi.org/10.1016/0006-3207(87)90064-4

Pulliam, H.R. (1973). On the advantages of flocking. *Journal of Theoretical Biology*, 38, 419–422.

Pulliam, H.R. (1988). Sources, sinks, and population regulation. *The American Naturalist*, 132, 652–661.

R Core Development Team. (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Relyea, R.A., Lawrence, R.K., & Demarias, S. (2000). Home range of desert mule deer: Testing the body size and habitat productivity hypotheses. *Journal of Wildlife Management*, 64, 146–153.

Rankin, D.J. & Kokko, H. (2007). Do males matter? The role of males in population dynamics. *Oikos*, 116, 335–348. doi.org/10.1111/j.0030-1299.2007.15451.x

Rieucau, G., & Giraldeau, L.A. (2011). Exploring the costs and benefits of social information use: an appraisal of current experimental evidence. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 366(1567), 949–957. doi:10.1098/rstb.2010.0325.

Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., Hayward, M.W., Kerley, G.I.H, Levi, T., Lindsey, P.A., Macdonald, D.W., Malhi, Y., Painter, L.E., Sandom, C.J., Terborgh, J., & Van Valkenburgh, B. (2015). Collapse of the world's largest herbivores. *Scientific Advances*, 1, e1400103.

Rodenhouse, N. L., Sherry, T.W., & Holmes, R.T. (1997). Site-dependent regulation of population size: a new synthesis. *Ecology*, 78, 2025–2042.

Rubanza, C.D.K., Shem, M.N., Otsyina, R., Bakengesa, S.S., Ichinohe, T., & Fujihara, T. (2005). Polyphenolics and tannins effect on in vitro digestibility of selected Acacia species leaves. *Animal Feed Science and Technology*, 119, 129–142.

Ruckstuhl, K.E. (2007). Sexual segregation in vertebrates: Proximate and ultimate causes. *Integrative and Comparative Biology*, 47, 245–257.

Ryan, S.J., Knechtel, C.U., & Getz, W.M. (2006). Range and habitat selection of African buffalo in South Africa. *Journal of Wildlife Management*, 70, 764–776.

Ryder, O.A. (1986). Species conservation and systematics: the dilemma of subspecies. *Trends in Evolution and Ecology*, 1, 9–10. doi.org/10.1016/0169-5347(86)90059-5

Saïd, S., Gaillard, J.-M., Duncan, P., Guillon, N., Guillon, N., Servanty, S., Pellerin, M., Lefeuvre, K., Martin, C., & Van Laere, G. (2005). Ecological correlates of home-range size in spring–summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland. *Journal of Zoology*, 267, 301–308.

Saïd, S., & Servanty, S. (2005). The influence of landscape structure on female roe deer home-range size. *Landscape Ecology*, 20, 1003–1012.

Sanz-Aguilar, A., Massa, B., Valvo, F.L., Oro, D., Minguez, E., & Tavecchia, G. (2009). Contrasting age-specific recruitment and survival at different spatial scales: a case study with the European storm petrel. *Ecography*, 32, 637–646. oi.org/10.1111/j.1600-0587.2009.05596.x

Schaller, G.B. (1972). The Serengeti Lion. Chicago: The University of Chicago Press.

Schaefer, J.A. (2006). Towards maturation of the population concept. *Oikos*, 112, 236–240. doi.org/10.1111/j.0030-1299.2006.13763.x

Schaefer, J.A., Veitch, A.M., Harrington, F.H., Brown, W.K., Theberge, J.B., & Luttich, S.N. (2001). Fuzzy structure and spatial dynamics of a declining woodland caribou population. *Oecologia*, 126, 507–514. doi.org/10.1007/s004420000555

Schoepf, I., Schmohl, G., König, B., Pillay, N., & Schradin, C. (2015). Manipulation of population density and food availability affects home range sizes of African striped mouse females. *Animal Behaviour*, 99, 53–60.

Schradin, C., Lindholm, A. K., Johannesen, J., Schoepf, I., Yuen, C-H., Konig, B., & Pillay, N. (2012). Social flexibility and social evolution in mammals: a case study of the African striped mouse (*Rhabdomys pumilio*). *Molecular Ecology*, 21, 541–553.

Seaman, D.E. & Powell, R.A. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, 77, 2075–2085. doi.org/10.2307/2265701

Shannon, G., Slotow, R., Durant, S.M., Sayialel, K.N., Poole, J., Moss, C., & McComb, K. (2013). Effects of social disruption in elephants persist decades after culling. *Frontiers in Zoology*, 10, 62.

Shier, D.M. (2006). Effect of family support on the success of translocated black-tailed prairie dogs. *Conservation Biology*, 20, 1780–1790.

Shizuka, D., & Farine, D.R. (2016). Measuring the robustness of network community structure using assortativity. *Animal Behaviour*, 112, 237–246. doi.org/10.1016/j.anbehav.2015.12.007

Shorrocks, B. (2007). The biology of African savannahs. New York, NY: Oxford University Press.

Shorrocks, B., & Croft, D.P. (2009). Necks and networks: a preliminary study of population structure in the reticulated giraffe (*Giraffa camelopardalis reticulata* de Winston). *African Journal of Ecology*, 47, 374–381.

Sih, A., Spiegel, O., Godfrey, S., Leu, S., & Bull, C.M. (2018). Integrating social networks, animal personalities, movement ecology and parasites: a framework with examples from a lizard. *Animal Behaviour*, 136, 195–205.

Silk, J.B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical transactions of the Royal Society of London. Series B*, 362, 539–559.

Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., & Cheney, D.L. (2009). The benefits of social capital: Close social bonds

among female baboons enhance offspring survival. *Proceedings: Biological Sciences*, 276, 3099–3104.

Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., & Cheney, D.L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, 20, 1359–1361.

Singh, N.J., Börger, L., Dettki, H., Bunnefeld, N., & Ericson, G. (2012). From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. *Ecological Applications*, 22, 2007–2020.

Smith, J.E., Kolowski, J.M., Graham, K.E., Dawes, S.E., & Holekamp, K.E. (2008). Social and ecological determinants of fission-fusion dynamics in the spotted hyaena. *Animal Behaviour*, 76, 619–636.

Sommer, S., & Ozgul, A. (2019). Demographic sources and sinks in mammals. In: Kelt, D.A., Heske, E.J., Sommer, S., Ozgul, Al. Orrock, J.L., Prugh, L., Pauli, J.N., Lambin, X., Oli, M.K., and Sollmann, R. Population dynamics and species interactions of mammals. *Journal of Mammalogy*, 100, 965–1007. doi.org/10.1093/jmammal/gyz017

Stanton, M.A., & Mann, J. (2012) Early social networks predict survival in wild bottlenose dolphins. *PLoS One*, 7, e47508. doi:10.1371/journal.pone.0047508.

Strauss, M.K.L., & Packer, C. (2013). Using claw marks to study lion predation on giraffes of the Serengeti. *Journal of Zoology*, 289, 134–142.

Strauss, M.K.L., Kilewo, M., Rentsch, D., & Packer, C. (2015). Food supply and poaching limit giraffe abundance in the Serengeti. *Population Ecology*, 57, 505–516.

Stutz, R.S., Bergvall, U.A., Leimar, O., Tuomi, J., & Rautio, P. (2018). Cohesiveness reduces foraging efficiency in a social herbivore. *Animal Behaviour*, 135, 57–86.

Taborsky, B. & Oliveira, R.F. (2012). Social competence: an evolutionary approach. *Trends in Ecology and Evolution*, 27, 649–714.

Tanzanian National Bureau of Statistics (TNBS). (2013). 2012 population and housing census. Ministry of Finance, Dar es Salaam, Tanzania.

Tavares, S.B., Samarra, F.I.P., & Miller, P.J.O. (2017). A multilevel society of herring-eating killer whales indicates adaption to prey characteristics. *Behavioral Ecology*, 28, 500–514.

Thaker, M., Vanak, A.T., Owen, C.R., Ogden, M.B., & Slotow, R. (2010) Group dynamics of zebra and wildebeest in a woodland savanna: Effects of predation risk and habitat density. *PLoS One*, 5, e12758. doi:10.1371/journal.pone.0012758

Thomas, C.D., & Kunin. W.E. (1999). The spatial structure of populations. *Journal of Animal Ecology*, 68, 647–657. doi.org/10.1046/j.1365-2656.1999.00330.x

Thompson, N.A., & Cords, M. (2018). Stronger social bonds do not always predict greater longevity in a gregarious primate. *Ecology and Evolution*, 8, 1604–1614. doi:10.1002/ece3.3791

Tingley, M.W., Wilkerson, R.L., Bond, M.L., Howell, C.A., & Siegel, R.S. (2014). Variation in home-range size of black-backed woodpeckers. *Condor*, 116, 325–340.

Tufto, J., Andersen, R., & Linnell, J. (1996). Habitat use and ecological correlates of home range size in a small cervid: The roe deer. *Journal of Animal Ecology*, 65, 715–724.

Turchin, P. (1998) Quantitative Analysis of Movement. Sinauer Associaties, Sunderland, Massachusetts, USA.

van der Jeugd, H.P., & Prins, H.H.T. (2000). Movements and group structure of giraffe (*Giraffa camelopardalis*) in Lake Manyara National Park, Tanzania. *Journal of Zoology*, 251, 15–21.

Vanderwaal, K.L., Wang, H., McCowan, B., Fushing, H., & Isbell, L.A. (2014). Multilevel social organization and space use in reticulated giraffe (*Giraffa camelopardalis*). *Behavioral Ecology*, 25, 17–26. doi.org/10.1093/beheco/art061

Venables, W.N., & Ripley, B.D. (2002). Modern Applied Statistics with S. Second edition. Springer: New York.

Waldram, M.S., Bond, W.J., & Stock, W.D. (2008). Ecological engineering by a mega-grazer: white rhino impacts on a South African savannah. *Ecosystems*, 11, 101–112.

Wang G., Thompson-Hobbs N., Boone R.B., Illius A.W., Gordon I.J., Gross J.E., & Hamlin K.L. (2006). Spatial and temporal variability modify density dependence in populations of large herbivores. *Ecology*, 87, 95–102.

Webber, Q.M.R., & Vander Wal, E. (2017). An evolutionary framework outlining the integration of individual social and spatial ecology. *Journal of Animal Ecology*, 87, 113–127.

Weladji, R.B., Gaillard, J.-M., Yoccoz, N.G., Holand, O., Mysterud, A., Loison, A., Nieminen, M., & Stenseth, N.C.. (2006). Good reindeer mothers live longer and become better in raising offspring. *Proceedings of the Royal Society B*, 273, 1239–44. doi:10.1098/rspb.2005.3393

Wells, J.V., & Richmond, M.E. (1995). Populations, metapopulations, and species populations: what are they and who should care? *Wildlife Society Bulletin*, 23, 458–462.

Western, D., & Lindsay, W.K. (1984). Seasonal herd dynamics of a savanna elephant population. *African Journal of Ecology*, 22, 229–244.

Wey, T., & Blumstein, D.T. (2012). Social attributes and associated performance measures in marmots: bigger male bullies and weakly affiliating females have higher annual reproductive success. *Behavioral Ecology and Sociobiology*, 66, 1075–1085. doi.org/10.1007/s00265-012-1358-8

Wey, T., Blumstein, D.T., Shen, W., & Jordan, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour*, 75, 333–344. doi.org/10.1016/j.anbehav.2007.06.020

White, G.C., & Burnham, K.P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study*, 46(Supplement), 120–138. doi.org/10.1080/00063659909477239

Whitehead, H. (1999). Testing association patterns of social animals. *Animal Behaviour*, 57, F26–29.

Whitehead, H. (2008a). Precision and power in the analysis of social structure using association. *Animal Behaviour*, 75, 1093–1099.

Whitehead, H. (2008b). Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis. University of Chicago Press, Chicago, IL, USA.

Whitehead, H. (2016). SOCPROG: Programs for analysing social structure. SOCPROG2.8, Halifax, Nova Scotia, Canada.

Whitehead, H., & Dufault, S. (1999). Techniques for analysing vertebrate social structure using identified individuals: review and recommendations. *Advances in the Study of Behavior*, 28, 33–74. doi.org/10.1016/s0065-3454(08)60215-6

Whitehead, H., Bejder L., & Ottensmeyer, C.A. (2005). Testing association patterns: issues arising and extensions. *Animal Behaviour*, 69, e1–e6.

Winnie, J. Jr., & Creel, S. (2007) Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. *Animal Behaviour*, 73, 215–225.

Wittemyer, G., Douglas-Hamilton, I., & Getz, W.M. (2005). The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour*, 69, 1357–1371.

Wolf, T.E., Bennett, N.C., Burroughs, R., & Ganswindt, A. (2018). The impact of age-class and social context on fecal glucocorticoid metabolite levels in free-ranging male giraffes. *General and Comparative Endocrinology*, 255, 26–31. doi:10.1016/j.ygcen.2017.09.022

Wolf, T.E., Ngonga Ngomo, A.-C., Bennett, N.C., Burroughs, R., & Ganswindt, A. (2018). Seasonal changes in social networks of giraffes. *Journal of Zoology*, 305, 82–87. doi:10.1111/jzo.12531

Wolff, J.O. (1994). More on juvenile dispersal in mammals. *Oikos*, 71, 349–352.

Young T.P., & Isbell L.A. (1991). Sex differences in giraffe feeding ecology: energetic and social constraints. *Ethology*, 87, 79–89.

Zannèse A., Morellet, N., Targhetta C., Coulon, A., Fuser, S., Hewison, A. J. M., & Ramanzin, M. (2006). Spatial structure of roe deer populations: Towards defining management units at a landscape scale. *Journal of Applied Ecology*, 43, 1087–1097. doi.org/10.1111/j.1365-2664.2006.01229.x